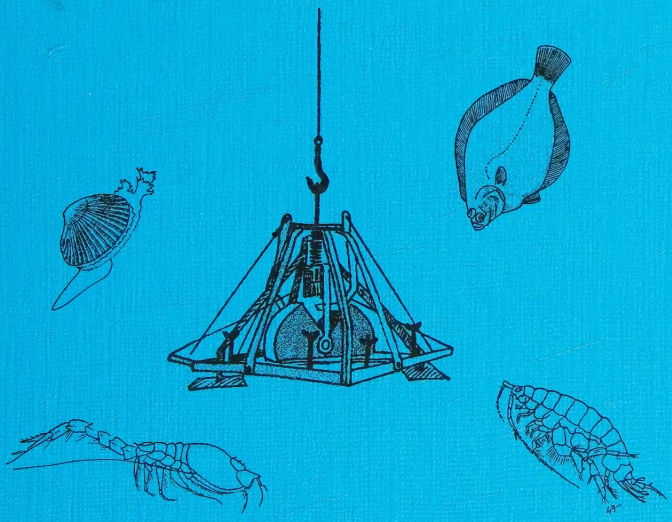
Structures and changes in soft bottom communities in the southern Baltic

Lars-Eric Persson



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Lund 1982

STRUCTURES AND CHANGES IN SOFT BOTTOM COMMUNITIES OF THE SOUTHERN BALTIC

LARS-ERIC PERSSON
FK, Ld

DISSERTATION
Lund 1982

Isn´t it better to tell it straight:
there is no truth -
only views!

Hjalmar Söderberg

LIST OF PAPERS

I Persson, L.-E. 1978. Spatial and temporal variations of juvenile macrofauna on a down-shore transect in Hanö Bight (southern Baltic). - Kieler Meeresforsch. Sonderheft 4, Kiel 1978. p 103-107.

II Persson, L.-E. 1982. Temporal and spatial variation in coastal macrobenthic community structure, Hanö Bay (southern Baltic). Manuscript.

III Persson, L.-E. 1976. Abundance and growth of a Cardium glaucum Bruguière population in Hanö Bight (southern Baltic. - Ophelia, 15(2): 163-174 (November 1976).

VI Persson, L.-E. 1982. Seasonal migration of Bathyporeia pilosa Lindström in the southern Baltic. Manuscript.

V Sundbäck, K. & Persson, L.-E. 1981. The effect of microbenthic grazing by an amphipod. Bathyporeia pilosa, Lindström. - Kieler Meeresforsch. Sonderheft 5, Kiel 1981, p 573-575.

VI Persson, L.-E. 1981. Long-term changes in population density of Diastylis rathkei, Krøyer (Cumacea) in different depths in the Hanö Bay, Southern Baltic. - Kieler Meeresforsch. Sonderheft 5, Kiel 1981. p 521-528.

VII Persson, L.-E. 1982. Macrobenthic associations of the Hanö Bight, southern Baltic. - Sarsia 67:2, 1982. (In press).

VIII Persson, L.-E. 1981. Were macrobenthic changes induced by thinning out of flatfish stocks in the Baltic proper? - Ophelia, 20(2): 137-152 (December 1981).

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TACK

Att denna avhandling kommit att handla om marin ekologi kan nog betraktas som en tillfällighet. Uppväxt i mellersta Skåne var min kunskap om och mitt intresse för havet ringa, när jag började studierna i Lund. Mitt intresse för djur och natur gjorde det så småningom naturligt att efter grundkurserna fortsätta med zooekologi. På grund av en, som jag då tyckte, olycklig omständighet uppsköts mina tre-betygsstudier en termin. Då detta var på den "gamla goda tiden", med jämlikhet i undervisningen av olika delar av biosfären innebar detta att jag hamnade på den marinbiologiska terminen. Efter en tid var jag fast.

Genomförandet av mitt avhandlingsarbete har möjliggjorts tack vare stöd från ett stort antal personer. Min handledare, Professor Per Brinck, Ekologiska avdelningens chef, har lagt ner ett stort arbete på att göra mina uppsatser inte bara läsbara utan i flera fall också tryckbara. Jag vill också tacka honom för hans hela tiden, trots ämnet, positiva inställning till mitt arbete. Hjälp med manusförfattandet har också getts av P.H. Enckell och Bo W. Svensson, vilket tacksamt ihågkommes.

De som känner till något om metodiken för bottenfaunaundersökningar vet att de oftast innebär ett stort laboratoriearbete med sortering av prover samt vägning och mätning av arter och individer. Jag har under de åtta år som Hanöundersökningarna pågått haft förmånen att ha Alena Ansheimer till hjälp. Den effektivitet och skicklighet hon arbetat med har gjort det möjligt att ta fram ett stort primärmaterial. Hennes tålamod, inte bara med tråkigt laboratoriearbete utan även många gånger vädervidriga provtagningsförhållanden, har varit beundransvärt. Dessa få rader kan endast delvis uttrycka den tacksamhet jag känner.

Det stora undersökningsprogrammet utfördes från fisketrålaren Zenitha (Sg 11) från Nogersund, och jag vill rikta ett varmt tack både till ägarna, Eric och Kalle Edwardsson, och de olika besättningsmedlemmar som följt med på dessa expeditioner. Dessutom tackar jag Eric och Siv för den gästfrihet och vänskap de visat under alla dessa år. Sven Hellström, Nyehusen, har hjälpt mig med mina provtagningar under senare år. Hans intresse och vilja att ställa upp såväl vardag som helgdag har underlättat mycket för mig.

Jag vill också tacka Kristina Sundbäck för många stimulerande diskussioner om dessa för en makrofaunaforskare osynliga organismer som kallas diatomeer. Till min kollega under senare år, Einar B. Olafsson, will jag rikta ett stort tack för många fruktbärande diskussioner om marinekologi, såväl i teori som praktik. Jag uppskattar också hans mod att ge sig in på den marina banan.

Undersökningarna har finansierats genom anslag från Statens Naturvårdsverk till Carl-Bertil Nordenberg, och jag är tacksam för att jag fick förmånen att under så lång tid självständigt arbeta inom samma ämnesområde. Ekonomiskt stöd har också erhållits från Fysiografiska sällskapet i Lund.

Färdigställandet av denna monografi har möjliggjorts tack vare stor hjälp av Steffi Douwes, som ritat figurer, Ulla Holmberg och Ylva Zachrison, som skrivit manuskript, och Gunilla Lindquist som klistrat och redigerat, ett stort tack alla. Görgen Göransson har gjort teckningarna på framsidan.

Slutligen, enligt bestämmelserna för forskarutbildningen skall djupare insikter i ämnet inhämtas via litteraturstudier, seminarier m m. Detta må vara viktigt, men när jag ser tillbaka på dessa år kan jag inte annat än finna att det som gett mig mest har varit de diskussioner som förts vid de dagliga stunderna vid kaffe- och lunchbord. Jag vill därför sist, men icke minst, tacka alla de som deltagit i dessa arbetspauser.

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BACKGROUND

The Baltic is one of the worlds largest brackish water areas. The salinity changes from 20 o/oo in the southwestern part to 6 o/oo in the northern part of the Baltic proper. It is a shallow sea with a mean depth of only 60 m, and a few deep basins separated by sills. An important feature of the physical system is the salinity stratification with a stable halocline at ~ 60 m depth maintained by a constant inflow of North Sea water. The primary halocline prevents a supply of oxygen to compensate for deficiency in the deep basins caused mainly by decomposition of sedimented organic matter. The stagnant anoxic bottom water is exchanged only by large influx of North Sea water. This occurs irregularly, as a result of certain meteorological conditions.

The Baltic ecosystem has been studied intensely, especially in the 1970s when the project 'Energy flow through the Baltic ecosystem' was carried out at the Askö laboratory, University of Stockholm. This resulted in a number of valuable publications giving much knowledge of the ecosystem. Some reviews have summarized the main results (Jansson 1972, 1978; Elmgren 1978).

My work in the southern Baltic was started in 1970 as a response to the increased concern for the environment. The aim of the project was to obtain knowledge of structure and changes of the benthic ecosystem. The stations in the Hanö Bight were chosen to be representative for areas fairly unaffected of local pollution.

SUMMARY OF RESULTS

METHOD

Most of my field work has been quantitative sampling of the benthic infauna. According to Baltic Standard Methods (Dyberg et al. 1976) a Van Veen grab should be used at macrofauna sampling. I preferred the heavier Smith-McIntyre grab, as the sediments in the Hanö Bight are sandy and compact. In the nearshore study of Bathyporeia pilosa a 28 cm^2 coresampler was used. The samples were preserved in 4 % neutralized formalin and stained with Rose Bengal before sorting.

RECRUITMENT TO THE NEARSHORE COMMUNITY (I)

Marine macrofauna is usually defined as animals retained by a screen of 1.0 x 1.0 mm mesh size. It was shown that the use of an additional sieve (0.5 x 0.5 mm) influenced the results considerably both temporally and spatially. Abundance and biomass increased towards the shore and were highest in the autumn. Variation was mainly due to the fact that the percentage of juveniles of species with long pelagic development increased when the depth decreased. Species with brood protection showed the same proportion in juveniles and adults at the three depths investigated (Fig. 1). It has been suggested that marine pelagic larvae have an ability to defer metamorphosis until they find a favourable habitat (Meadows & Campbell 1972, Gray 1974). Therefore, different settling intensity could be an explanation for the differences found in numbers of juveniles.

STRUCTURES AND CHANGES IN THE NEARSHORE COMMUNITY(II)

The distribution of species along the transect (5, 10, 17 m) was determined by exposure and temperature. The seasonal variations in abundance were connected with the recruitment of juveniles except for Bathyporeia pilosa which migrated to shallower areas in summer. Seasonal changes due to recruitment are common in temperate waters. The annual changes were small both as regards species composition and abundance. This may be due to the low number of species and their eurytopic occurrence.

Differences were found in the size frequency distribution of molluscs at the three depths. The cause for the higher number of juveniles at the 5 m depth might be either that the larval settlement is equal at all depths, but that the mortality of the first stages differs due to negative interactions of adult individuals (see Petersen and Andre 1980), or that there is a preferential settling of larvae and a migration of grown-up individuals. The problem can be solved by quantitative sampling of newly settled larvae.

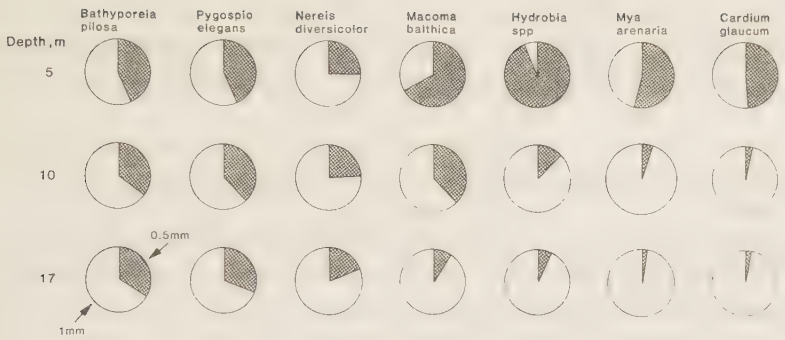

Fig. 1. Mean values of additional abundance from a 0.5 mm sieve, (juveniles) in per cent of total abundance (1.0 + 0.5 mm sieve). Dominant species with brood protection (B.p.) and semi-pelagic (P.e., N.d.) and pelagic development (M.b., H.spp., M.a. and C.g.) are shown.

ANNUAL AND SEASONAL VARIATION IN GROWTH RATE OF CARDIUM GLAUCUM (III)

One of the dominant species along the transect is C. glaucum. It had a very successful settlement in 1972 and it is suggested that this resulted from a combination of high temperature and favourable currents. The temperature dependance of growth is shown by the growth rate which is higher at the 10 m depth than at the 17 m depth. The main part of the growth took place in July and August, but slow growth continued in October through February.

FOOD LIMITATION AND MIGRATION OF BATHYPOREIA PILOSA (IV)

The main part of the population lives at depths of 2-3 m in summer and autumn and 4-5 m in winter and spring. Migration in Crustacea is usually reported to be temperature dependent, including a movement to warmer places. In the investigated area, however, winter temperature was equally low at all depths. B. pilosa feeds on microbenthic diatoms and probably vegetable debris. Data in literature on seasonality of diatoms seem to intimate that the migration is induced by the lowered food availability in shallow water in winter. In deeper water the individuals consume less energy as the sediment is more stable which permits them to remain inactive. This conclusion is supported by studies of a

B. pilosa population on a sheltered sandbank in the Sound (Persson & Sundbäck unpubl.). In this area (0.5 m depth) the density remained high during winter in spite of temperatures below zero.

DENSITY DEPENDENT GRAZING EFFECTS OF BATHYPOREIA PILOSA (V)

High densities of B. pilosa lower both biomass and primary production of microbenthic diatoms. In spring 1980 it was shown experimentally that there was a density dependent mortality of juveniles hatching. This can be explained by food competition or intraspecific disturbances in dense populations. In the autumn of 1979 we found that Bathyporeia selectively ingests Cocconeis spp. In 1980 the relative abundance of Cocconeis was lower and there was no such food selection. The reason may be the seasonal variation in biomass of diatoms and the general behaviour of grazers. When food is abundant the grazer can afford to be selective, but not when food is scarce (Stenseth 1981).

JUVENILE MORTALITY AND DENSITY CHANGES IN DIASTYLIS RATHKEI (VI)

In the investigations along the nearshore transect (Paper II) one species varied between the years in abundance, viz. Diastylis rathkei. Increasing population densities were found up to 1975 after which they decreased. In order to ascertain the generality of this variation the results from seven stations in depths of 10-58 m were analyzed. It was found that the population changes were similar at all stations down to 38 m depth. At 43 m depth annual population changes were small and at 58 m depth three density peaks were found in the eight years studied. Analyses showed significant positive correlations between high surface temperature in winter (January-March) and high population density the following summer at stations down to 38 m depth but not in the deeper stations. This seems reasonable, since in winter the Baltic water is homoitherm down to about 40 m depth. It is suggested that the low temperatures negatively affect the survival of the newly hatched juveniles. The population changes at the 58 m depth were found to be connected with the oxygen content of the bottom water, e.g. the density decreased after influx of new water. The reason is most probably that the new water lifts up

the oxygen deficient bottom water which negatively influences the fauna in the surroundings of the basin.

CONTROLLING FACTORS OF SPATIAL AND TEMPORAL DISTRIBUTION OF COMMUNITIES IN THE HANÖ BIGHT, SOUTHERN BALTIC (VII)

In order to identify distributional patterns of the species and determine the controlling environmental factors, an objective community analysis of the macrozoobenthos in the Hanö Bight was carried out at 46 randomized stations, which were sampled in August 1975. The highest number of species was found between 5-19 m and the highest density and biomass at 20-29 m. The distribution of the species was controlled by abiotic factors, e.g. temperature, salinity and sediment composition. The community analyses gave six or seven assemblages depending on the method used. These assemblages represented in most cases separate areas of the Bight. Comparison of the density and distribution pattern found with earlier data suggests the theory of global stability to be applicable for macrobenthic fauna above the halocline in the Baltic. This implies that only one stable point exists in the community and adjustment to this point takes place after a perturbation.

REDUCED PREDATION AND MACROBENTHIC INCREASE IN THE BALTIC (VIII)

As no general trend in population changes of macrozoobenthos became evident after 5-6 years of monitoring, Cederwall & Elmgren (1980) made a comparison with the 1920s (Hessle 1924) in the middle part of the Baltic proper. They found a more than fourfold increase in biomass above the halocline. They suggested that this might be a result of the eutrophication of the Baltic. This theory is rejected for the following reasons:

1. In the area south of Gotland no biomass increase of macrozoobenthos seems to have occurred since the 1950s, but a significant increase was stated for the 1920s through the 1940s.
2. Nutrient pollution has increased mainly after the 1940s.
3. No structural changes, generally connected with organic pollution, have occurred in the Baltic communities since the 1920s.

Another explanation to the biomass increase was suggested, viz. decreased predation pressure from exploited flatfish popula-

tions. It is usually thought that the fish populations in the Baltic have been steadily increasing. Old literature data, however, shows that this does not apply to all species. Investigations in the 1910s showed that the southern Baltic had very large populations of three flatfishes, viz. flounder, plaice and dab. It is reasonable to assume densities 10-100 times higher than today. These species are feeding on macrozoobenthos and the high densities in the 1910s resulted in severe competition for food and stunted growth. After heavy exploitation of these populations in the 1920s and early 1930s the populations were reduced and simultaneously the growth rate increased to the same level as in the 1970s.

Experimental as well as field studies of predator-prey relationships in the aquatic environment have given opposing results. Recently Thorp & Bergey (1981) reported that no evidence of population changes of benthos could be found at different densities of a predatory fish. However, they hypothesized a possible impact on a simple benthic system by a guild of predators. In the Baltic we have a simple benthic ecosystem and the three flatfishes were exploiting all dominant benthic species.

I conclude that the increase of macrobenthic biomass in the Baltic proper since the 1920s is a result of the reduced predation pressure.

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Spatial and temporal variations of juvenile macrofauna on a downshore transect in Hanö Bight (Southern Baltic)

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Abstract

The intention was to study recruitment of benthic macrofauna to an exposed shore. Two mesh-sizes (1.0 and 0.5 mm) were used. The additional abundance and biomass in the finer sieve show both temporal and spatial variations. Maximum values were found in the autumn and at the shallowest station (5 m). The reasons for this are discussed.

Zusammenfassung

Räumliche und zeitliche Variationen der juvenilen Makrofauna auf einem Schnitt im unteren Küstenbereich der Hanö Bucht (südliche Ostsee)

Ziel war es, die Neubesiedlung an benthischer Makrofauna an einem exponierten Strand zu untersuchen. Zwei Maschenweiten wurden benutzt (1.0 und 0,5 mm). Die größere Häufigkeit und Biomasse im feineren Sieb lassen zeitliche und räumliche Variationen erkennen. Die höchsten Werte wurden im Herbst und an der flachesten Station (5 m) gefunden. Die Ursachen dafür werden diskutiert.

Introduction

Comparisons between quantitative marine benthic studies are difficult for several reasons, e.g. 1) the variety of samples used, 2) the different mesh-sizes used in the sieving screens and 3) the temporal variations of the fauna. The importance of the mesh-size has been dealt with for mud bottoms (REISH, 1959; McINTYRE, 1961; ANKAR, 1976) and mixed mud and sandbottoms (DRISCOLL, 1964).

Material and methods

Sampling was performed at 5, 10 and 17 m depth along a transect in the Hanö Bight (Southern Baltic) between August 1974 and September 1976 (for physiochemical description see PERSSON, 1976). Sampling was carried out twelve times at varying intervals. Ten or twenty samples were taken on each occasion with a 0.1 m^2 Smith–McIntyre grab. Half of the samples were sieved through both 1.0 and 0.5 mm screens, while the other half through a 1.0 mm screen only. The sieve residues were preserved in 4% buffered formalin.

Results

The use of a 0.5 mm screen increases the number of macrofauna species found only to a small degree. The mean number of species increased only between 0.4 and 1.1 units for the three sampling sites.

The increase in abundance found by using a 0.5 mm screen was very different for the three depths. The highest number of juvenile specimens were found at 5 m depth

where the mean increase was 52.0 ± 5.8 % of total abundance 1.0 + 0.5 mm). This was due mainly to three species, *Macoma balthica*, *Hydrobia ulvae* and *Bathyporeia pilosa*. At 10 m depth the mean increase was 23.6 ± 4.1 %, most of it coming from *M. balthica*, *H. ulvae* and *Nereis diversicolor*. At 17 m depth only a minor part of total abundance was found in the 0.5 mm sieve (6.8 ± 1.3 %). The four species mentioned contributed with an almost equal number of individuals, (Fig. 1).

In a *Macoma balthica* community containing heavy molluscs only a small amount of the total biomass came from the 0.5 mm sieve. There were however great differences between the three depths investigated. The percentage increase was higher for the lower depths towards the shore. The highest biomass found in the 0.5 mm sieve was 11.96 g/m² at 5 m and the lowest 0.02 g/m² at 17 m (both from September 1975)

The variation of the addition of individuals from the 0.5 mm sieve was very small for the 17 m depth and very high for the 5 m depth during the sampling period, (Fig 2). During

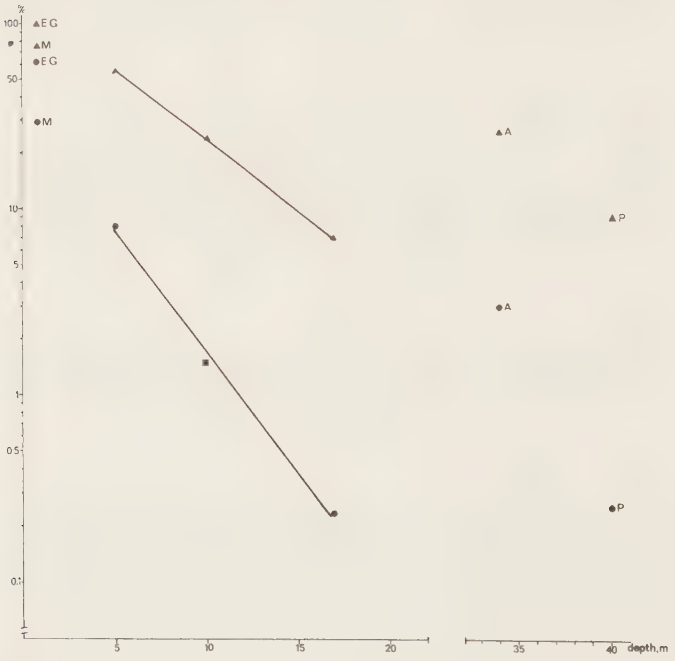

Figure 1

Mean values of additional abundance (▲) and biomass (●) in the 0.5 mm sieve per cent of total values (1.0 & 0.5 mm) for the three depths. Letters refers to E.G. = Elmgreen & Ganning, M. = Muus, A. = Ankar, P. = Persson.

the first year the 5 and 10 m depths both exhibited maximum abundance of juveniles in the autumn and a minimum abundance in the winter. During the second year the values were however influenced by the high number of juveniles settling in the summer and autumn 1975, especially at 5 m with a delayed increase at 10 m depth. The increase at 17 m depth in spring 1976 was not connected to the 5 and 10 m peaks, as it depended on a high number of juveniles from winter-reproducing species (*Diastylis rathkei*, *Pontoporeia affinis*).
As regards the 1.0 mm samples the 10 and 17 m depths showed similar abundance except for autumn values in 1976.

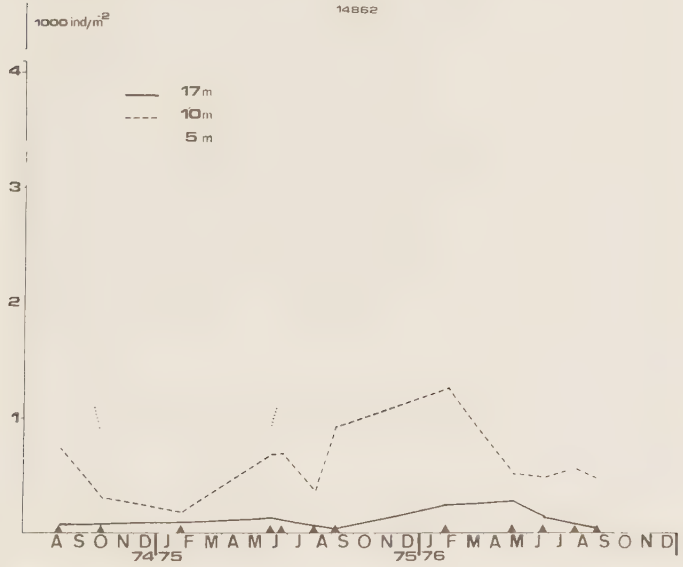

Figure 2

Additional abundance in the 0.5 mm sieve at the three depths, Aug. 1974–Sept. 1976. ▲ = sampling time

Discussion

The values indicate that the numbers of macrofauna species in Baltic sand bottoms are correctly estimated with a 1.0 mm sieve.
The number of specimens and biomass caught in the finer sieve increases with decreasing depth within the interval 5-17 m. SEGERSTRALE (1960) mentioned that the number of small *Macoma balthica* increased in shallow water. The values from other investigations inserted in Fig. 1 all show a higher number of juveniles in shallow water. The high values of ANKAR (1976) in deeper areas may be explained by the high number of juvenile *Pontoporeia affinis* at this time of the year (June) in this area.

The differences, showing higher abundance of juvenile specimens in shallow water may have different causes, 1) the species has a non-pelagic development and different number of juveniles reflect the numbers of adults or differences in fecundity, 2) the differences are due to settling intensity of pelagic larvae, 3) the settling intensity is equal in size but mortality of the first benthic stages (not retained by a 0.5 mm sieve) is different.

Of the three main taxa the Amphipoda have a non-pelagic development with brood care, and there was good consistency between the number of the dominating species *Bathyporeia pilosa* from the two sieves. This was to some extent also true for the Polychaeta, where *Nereis diversicolor* has a semi-pelagic development, but not for the Mollusca which have a pelagic development.

Many pelagic larvae have the possibility of choosing their substratum and deferring metamorphosis until they find it (THORSON, 1966; MUUS, 1973), but it seems difficult to believe that they can discriminate between sites with almost the same type of sediment and with adult populations of about the same size.

Different settling intensity can however be of non-active origin induced by direction and strength of currents. According to temperature measurements the area seems to be influenced by the same watermass, even if there is a tendency for up-welling which may cause a transport of larvae towards the shore.

Different mortality rates for the first benthic stages can be explained by shortage of food or heavier predation in deeper areas. The fact that macrobenthic biomass becomes somewhat higher with depth along this transect (PERSSON unpubl.) and benthic primary production becomes smaller with depth (GARGAS, 1970) points to food competition as an explanation for the spatial differences. This effect es reached later in shallow water, but in time to almost cancel out the differences before the specimens are caught in the 1.0 mm screen.

The temporal variation in the differences between the two sieves depends on the type of community studied. A community dominated by Molluscs ought to have a peak of juveniles in autumn (BERG, 1973; JANSSON, 1974), whereas a community from deeper areas in the Baltic dominated by Crustacea with winter reproduction (*Pontoporeia sp, Diastylis rathkei)* has a peak in the spring.

It is evident that in studies of Baltic macro-fauna the mesh-size has to be determined with regard to the temporal and spatial variations in the sampling area, which in turn seems to be highest in shallow water.

Acknowledgements

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TEMPORAL AND SPATIAL VARIATION IN COASTAL MACROBENTHIC COMMUNITY STRUCTURE, HANÖ BAY (SOUTHERN BALTIC)

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ABSTRACT

Quantitative (0.1 m^2) samples of benthic macrofauna were taken at three depths (5, 10, 17 m) off the eastern coast of Scania, southern Baltic, in the period April 1973 - August 1978. Altogether 20 sampling cruises were carried out. Spatial and temporal species composition, abundance and biomass were compared. Number of species increased significantly with increasing depth. Zonation of species were due to their zoogeographical origin and capacity to withstand exposure. Abundance was highest at 5 m depth whereas biomass increased with depth due to the dominance of large bivalves. Variation in abundance within years was large at all three depths and connected with reproductive recruitment for all species except Bathyporeia pilosa which migrated towards the shore in summer.

INTRODUCTION

Many studies have dealt with the down-shore zonation of benthic macrofauna, but most of them were carried out in areas influenced by the tide and many were restricted to the intertidal part. Sublittoral studies have been made by e.g. Clarck & Milne (1955), McIntyre & Eleftheriou (1968), Gage (1974), Watling (1975), Dörjes (1976) and Larsen (1979).

In the Baltic the near-shore zonation was studied by e.g. Segerstråle (1933), Bagge et al. (1965), Särkkä (1969) and Berg (1973). They report on rather sheltered areas, with high silt--clay content in the sediment. In most cases, however, only a few surveys were made and annual fluctuations were neglected. Outside the Baltic attention has been paid to seasonal as well as annual fluctuations of coastal macrobenthic communities both in temperate (Levings 1975, Buchanan et al. 1978, Kiørboe 1979) and subtropic (Petersen 1975, Poore & Rainer 1979, Stephenson 1980) areas. Knowledge of the variation of the community structure and the population dynamics is important, particularly for the evaluation of data from pollution investigations (Maurer et al. 1979).

Exposure, temperature and substrate are major abiotic factors which interact and control species distribution and community dynamics of marine shallow water fauna. At an exposed coast the stress on the benthic animals is increasing towards the shore due to the sediment instability and temperature variability. This may affect the community structure by a lower diversity, higher temporal fluctuations and more short-lived populations.

The aim of this study was to examine spatial, seasonal and annual variations in the near shore community, in order to be able to trace factors important in structuring these communities in the southern Baltic.

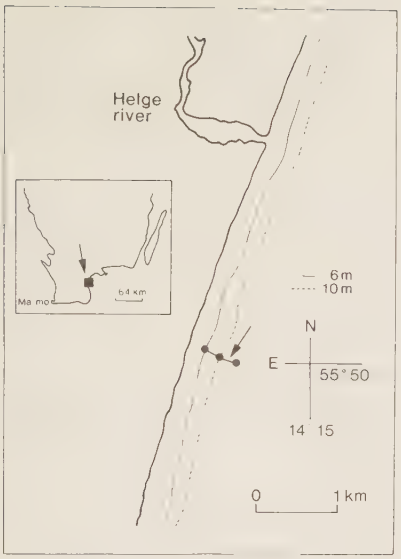

Fig. 1. Study area with sampling stations on the eastern coast of Scania, southern Baltic.

METHODS

Sampling was conducted with a 0.1 m^2 Smith-McIntyre grab at three depths (5, 10 and 17 m) along a transect extending 700 m from the shore in eastern Scania, southern Sweden (Fig. 1). The position of the stations were determined by aid of echosounder, decca navigation and radar.

Altogether 20 sampling cruises were performed between April 1974 and August 1978. Five or 10 replicates were taken at 5 and 10 m depths and 5, 10 or 20 at 17 m depth, giving 630 samples. A 1.0 mm sieve was used, and the sieve residues were preserved in 4 % buffered formalin. Before sorting, the samples were stained with Rose Bengal.

Biomass was determined as formalin wet weight after blotting on a filter paper. Bivalves were opened to remove water from the mantle cavity. Biomass of Pygospio elegans was estimated by using a "mean value" of 1.0 mg/ind. as proposed by Muus (1967).

Subsamples for sediment analyses were taken from the last grab at each sampling time. Particle size was determined by dry sieving, and the organic content was measured as ignition loss at 550° C after two hours.

In 1976 and 1977 temperature was measured in the surface and bottom water at the three depths during May-October. In 1976 a maximum and minimum thermometer was read off every week, and in 1977 a spring operated Ryan instrument was used. Data on velocity and direction of wind from the island of Hanö was used (source SMHI, Swedish Meteorological and Hydrological Institute).

The diversity of the fauna was calculated by means of four indices, of which Margalefs index d (Margalef 1958) and Sanders rarefaction index (Sanders 1968) express species richness, whereas the Shannon index H' (Shannon & Weaver 1963) and the eveness index E (Pielou 1966) reflect dominance diversity.

The affinity between the three depths was calculated both as species and dominance similarity. In the first case Czekanowski's coefficient was used,

$$C_s = \frac{2\ w}{(a + b)}$$

where a is the number of species in sample A, b is the number of species in sample B and w is the number of species common to both samples.

In the second case the percentage similarity coefficient was used. This is represented by the sum of the smaller dominance values for species common to both samples. As this measure gives higher importance to dominant species it was calculated both with and without the polychaet Pygospio elegans when comparing the mean dominance values of the three depths and only without P. elegans when comparing similarity within and between depths in time.

STUDY AREA

The sediment composition was about the same for the three depths, with fine to very fine sand as the dominating fraction (Table 1). The coefficient of variation was higher for the two sand fractions at 5 and 10 m depth, indicating a more unstable sediment. The silt-clay content was low with the highest value at 17 m.

Ignition loss was significantly higher at 10 m depth than at 5 and 17 m depth ($p < 0.001$ and < 0.05). No significant difference was found between the 5 and 17 m depth ($p = 0.062$).

Salinity data were extracted from measurements made by the Swedish Fishery Board (Blad & Rasmussen 1978) and ranged between

TABLE 1

Mean grain-size distribution (eight series) and ignition loss (twelwe series) from the three depths.

Depth	> 2.0 mm	1.0 - 2.0 mm	0.5 - 1.0 mm	0.2 - 0.5 mm	0.06 - 0.2 mm	< 0.06 mm	I %
5 m	0.39 ± 0.06	1.04 ± 0.31	1.26 ± 0.69	28.83 ± 8.39	67.21 ± 9.11	1.64 ± 0.93	1.05 ± 0.08
10 m	0.34 ± 0.17	0.19 ± 0.06	0.54 ± 0.15	27.86 ± 8.95	69.72 ± 8.73	1.44 ± 0.38	1.99 ± 0.15
17 m	0.25 ± 0.12	0.27 ± 0.11	0.72 ± 0.17	22.51 ± 4.04	72.12 ± 3.27	4.12 ± 2.72	1.52 ± 0.25

7.5 ‰ in May and 9.3 ‰ in August, 1975. According to the authors the higher values were connected with upwelling.

In summer 1977, the temperature in the surface water ranged from 6° C to 17.5° C and from 3.5° C to 15.5° C at 17 m depth (Fig. 2). The data on the wind direction show a clear connection between direction and upwelling of cold deep water. In the second half of June the surface temperature decreases from 16° C to 7° C in four days with southwesterly winds. For 1977 three to four periods of upwelling could be detected. According to Johansson (1977) upwelling occurred 3-5 times a year in summer during the years 1973-75.

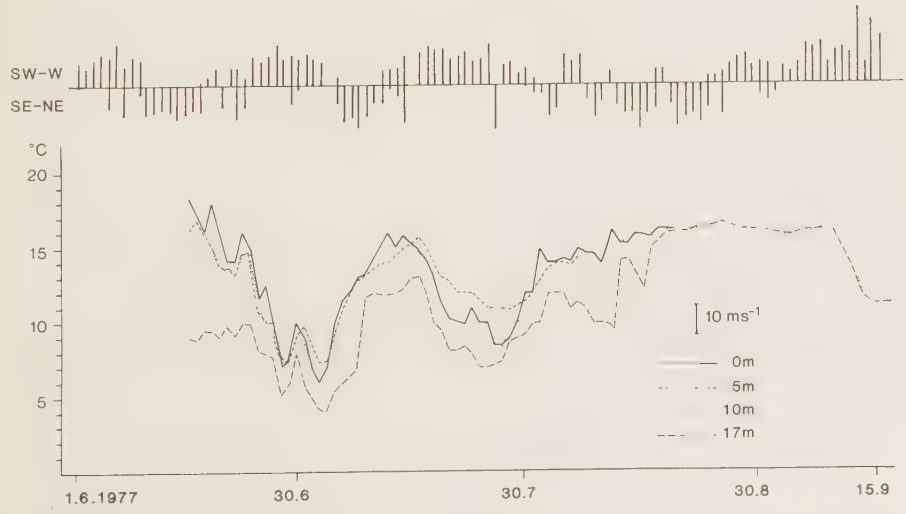

Fig. 2. Temperature from surface and bottom water at the three depths investigated in summer 1977. Data on the force and direction of the wind are inserted.

In 1976 the difference in temperature between the three depths was greatest in July when the 5 m depth had a surplus of 61.5 and 112.0 day-degrees compared with the 10 and 17 m depths. In August and September the difference decreased to 28 - 57 and 21 - 39 day-degrees respectively. In 1977 July was cold and the mean values lower than in 1976, but the differences between the three depths were of the same magnitude. The stratification is usually broken down in September.

RESULTS

SPATIAL VARIATION

Number of species, abundance and biomass

A total of 23 species and 5 undetermined taxa were found. Crustacea was the most diverse group comprising 14 species compared to 6 and 4 for molluscs and annelids, respectively (Table 2). The table shows that the number of species found decreased with decreasing depth. Significant differences between the three depths were found in mean number of species/cruise and mean number of species/replicate (0.1 m^2), ($p < 0.001$, Students t).

The polychaet Pygospio elegans was the most frequent species occurring in all 630 samples taken. Macoma balthica ranked second, absent only in two samples at the 5 m depth, and Nereis diversicolor third.

Mean density of macrofauna was highest at 5 m depth but the differences found were not significant due to great variance. Pygospio elegans was the dominant species and accounted for about 70 % of the density. When this species was excluded the mean density at 10 m depth was found to be significantly higher than at 5 and 17 m depth ($p < 0.01$ and < 0.05).

The dominant species were distributed in three groups with abundance maxima at different depths (Fig. 3). The group showing highest abundance at 17 m depth had a particularly low abundance at 5 m depth.

The mean biomass was highest at 17 m depth and then decreased towards the shore (Table 2). But only the differences between the 5 m depth and the two others were significant ($p < 0.001$). The mean values mainly express the variation of the weight of molluscs, which made up 93 (17 m), 89 (10 m) and 79 % (5 m) of the

TABLE 2

Number of species found, with mean values of abundance (ind./m^2) and biomass (g/m^2) calculated for the 20 sampling series. Frequency is presented as percentage occurrence in series (F^{20}) and grabs ($F^{0.1}$).

Species	5 m $\bar{N}$	5 m $\bar{B}$	5 m F^{20}	5 m $F^{0.1}$	10 m $\bar{N}$	10 m $\bar{B}$	10 m F^{20}	10 m $F^{0.1}$	17 m $\bar{N}$	17 m $\bar{B}$	17 m F^{20}	17 m $F^{0.1}$
INSECTA												
Chironomidae spp.	0.5	0.001	15	4.5	0.1	0.000	5	0.5	0.3	0.000	20	2.0
NEMATODA												
Nematoda spp.		q			0.2	0.000	5	1.0	0.7	0.000	10	1.0
NEMERTINI												
Nemertini spp.	0.6	0.002	20	3.5	4.4	0.026	70	30.0	3.1	0.021	75	24.0
PRIAPULIDA												
Halicryptus spinulosus Siebold					0.2	0.001	5	2.0	6.5	0.064	80	34.5
Varia Σ	1.1	0.003			4.9	0.027			11	0.085		
ANNELIDA												
Harmothoe sarsi (Malmgren)	0.1	0.000	5	0.5	11.6	0.004	30	11.5	13	0.095	65	20.5
Nereis diversicolor O.F. Müller	132	1.898	100	92.5	241	3.596	100	99.5	83	1.284	100	97.5
Pygospio elegans Claparède	4803	4.803	100	100	3480	3.480	100	100	3606	3.606	100	100
Oligochæta spp.	1.4	0.001	35	9.5	73	0.076	95	855	135	0.130	100	99.0
Annelida Σ	4937	6.702			3806	7.156			3837	5.115		
CRUSTACEA												
Praunus inermis (Rathke)	0.1	0.000	5	0.5								
Neomysis integer (Leach)	0.6	0.004	20	5.0	0.5	0.001	30	4.0	1.1	0.005	25	4.5
Diastylis rathkei Krøyer	2.5	0.009	70	21.5	25	0.076	100	69.0	53	0.224	100	79.5
Mesidotea entomon L.	0.1	0.004	5	0.5	0.1	0.003	10	1.0	1.1	0.177	55	6.8
Idotea balthica (Pallas)	0.2	0.005	10	1.5	0.2	0.006	15	2.0	0.4	0.003	25	2.5
Iaera albifrons coll. Leach					0.1	0.000	5	0.5	0.1	0.000	5	0.5
Eurydice pulchra Leach	0.3	0.000	15	2.5								
Gammarus oceanicus Segerstråle									0.1	0.000	5	0.5
Gammarus salinus Spooner	1.2	0.008	40	7.0	1.6	0.017	55	9.0	6.9	0.074	90	26.0
Calliopius rathkei (Zaddachi)	0.1	0.000	5	0.5	0.1	0.000	5	0.5	0.1	0.000	10	1.0
Bathyporeia pilosa Lindström	542	1.242	100	95.5	54	0.125	95	75.0	37	0.103	95	70.5
Corophium volutator (Pallas)	0.6	0.003	40	5.5	7.2	0.045	80	32.5	5.1	0.034	90	24.0
Pontoporeia affinis Lindström	1.2	0.004	55	11.0	21	0.070	100	65.0	36	0.160	100	80.3
Crangon crangon L.	1.1	0.092	45	9.0	0.5	0.014	40	5.0	1.0	0.023	55	9.0
Crustacea Σ	550	1.371			110	0.357			142	0.803		
MOLLUSCA												
Hydrobia spp	130	0.156	100	77.5	1200	0.883	100	100	878	1.470	100	100
Theodoxus fluviatilis					0.1	0.001	5	0.5	0.1	0.002	10	1.0
Mytilus edulis L.	0.4	0.007	25	3.5	2.4	0.082	65	18.0	14	1.570	100	40.0
Cardium glaucum Bruguière	32	2.129	80	46.0	57	17.170	100	94.0	58	11.407	100	91.0
Macoma balthica (L.)	476	25.833	100	99.0	408	41.538	100	100	340	61.256	100	100
Mya arenaria L.	43	1.518	100	66.0	137	12.118	100	95.5	130	9.016	100	96.5
Mollusca Σ	681	29.643			1805	71.792			1420	84.721		
Mean value/m^2	6169	37.719			5726	79.332			5410	90.724		
Mean value of species/series ± S.E.		11.21 ± 0.44				14.26 ± 0.42				15.95 ± 0.60		
Mean value of species/0.1 m^2		6.66 ± 0.30				10.02 ± 0.19				11.29 ± 0.22		

total biomass. The variation in molluscan biomass agrees with variation in abundance except for Macoma balthica which has a reversed pattern (Fig. 3). This is due to the change in population structure with increasing depth (Fig. 4).

Diversity and similarity

Diversity measured as dominance diversity (H' and E) was highest at the 10 m depth, but at the 17 m depth when measured as species richness (d and rarefaction) (Table 3, Fig. 5). The values from

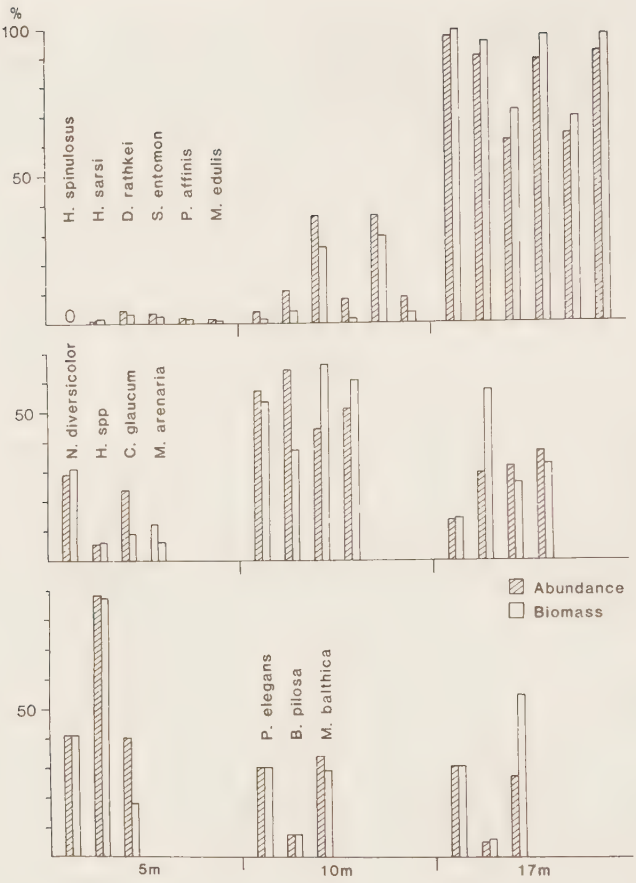

Fig. 3. Percentage distribution of abundance and biomass for dominant species at the three depths investigated. Mean values of 20 sampling series.

the 5 m depth were significantly lower than those of 10 and 17 m depths, which differed significantly only with respect to their d-values. The rarefaction curves overlap slightly more between the 10 and 17 m depths than between the 5 and 10 m depths, and below 2000 ind. the mean value for the 10 m depth lies within the range of the 17 m values.

The similarity between depths based on the mean data for all cruises (Table 2) was rather high both with presence/absence and dominance data, range 72 - 93 %. However, when dominance similarity was calculated without Pygospio elegans only the similarity between the 10 and 17 m depths remained high, 82 %. The values

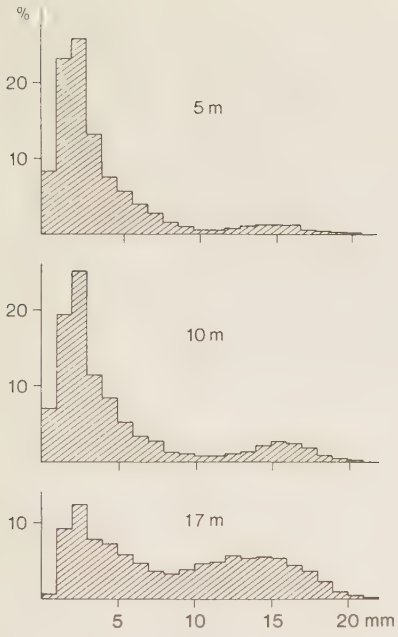

Fig. 4. Length-frequency of Macoma balthica at the three depths investigated. The histograms represent mean values of 20 sampling series.

TABLE 3

a. Mean values of diversity indices of the 20 sampling series, calculated both with and without the dominating species Pygospio elegans. b. Significance levels of comparisons between depths, x = $p < 0.05$, xx = $p < 0.01$, xxx = $p = 0.001$.

a.

	5 m		10 m		17 m	
	tot.	- P.e.	tot.	- P.e	tot.	- P.E.
H'	1.20	1.68	1.79	2.05	1.75	2.35
E	0.35	0.51	0.47	0.55	0.43	0.59
d	1.21	1.31	1.58	1.63	1.91	2.04

b.

	total values			without P. elegans		
	5/10	5/17	10/17	5/10	5/17	10/17
H'	xxx	xxx	-	xxx	xxx	-
E	xxx	x	-	x	xx	-
d	xxx	xxx	xxx	xxx	xxx	xxx

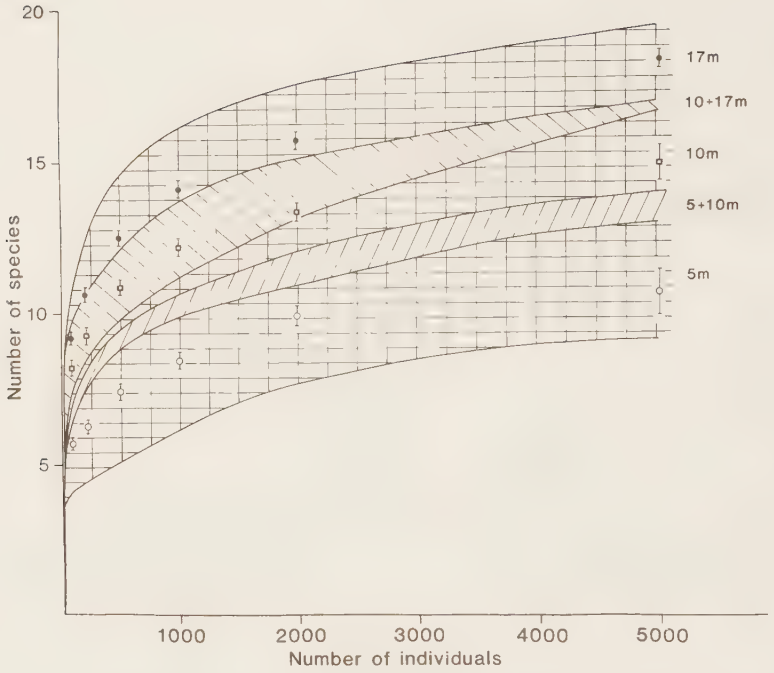

Fig. 5. Rarefaction curves based on data from 20 sampling series. Mean values ± S.E. and range are marked.

for the 5 m depth dropped to 44 and 46 %. As can be seen from Table 2 this mainly depends on the high abundance value of Bathyporeia pilosa and the low dominance value of Hydrobia spp. at this depth.

TEMPORAL VARIATION

Number of species, abundance and biomass

There were no significant differences in number of species/cruise or replicate between years or seasons in the three depths. New species were added during the whole sampling period at 5 and 10 m depths, but only until cruise 9 at 17 m depth (Fig. 6). This may be due to either a higher number of rare species or to short-time invasion by adults or recruits at the two shallower depths.

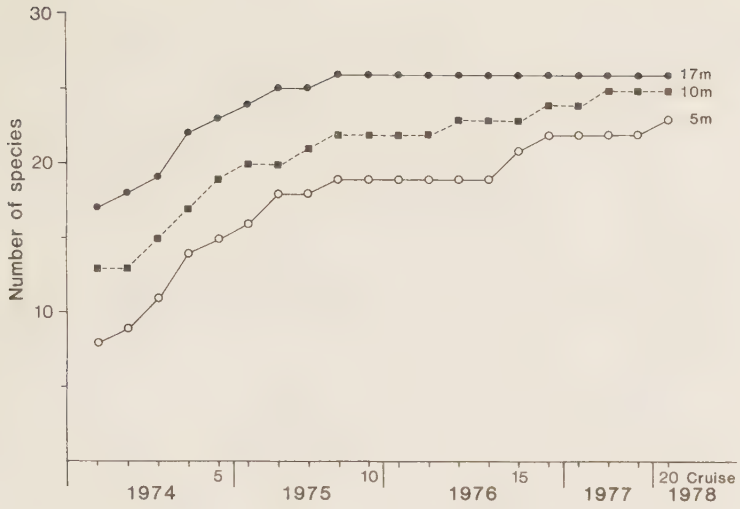

Fig. 6. Cumulative number of species with time found at the three depths.

Variation in abundance within years was large in all three depths both for total values and when P. elegans was excluded (Fig. 7). Total abundance was highest in summer or spring but the differences found were not significant due to low number of samples in some seasons and large variance between years.

When P. elegans was excluded significant difference was found between high winter and low summer values (Anova, $p < 0.05$) at the 5 m depth.

The variation in total abundance is mainly due to the variation of the dominant species P. elegans, which shows a clear seasonality with high summer values (Fig. 8a). Both the highest and the lowest density found during the three years was recorded at the 5 m depth. Bathyporeia pilosa showed high density in winter and spring at all the three depths (Fig. 8b). Especially at 5 m depth abundance was high and B. pilosa had in February through March (1975-77) a dominance value between 60 and 76 % (P.elegans excluded). At the 10 and 17 m depths the corresponding value only once exceeded 7 %.

Due to the dominance of long-lived molluscs no significant variations in biomass within or between years was found.

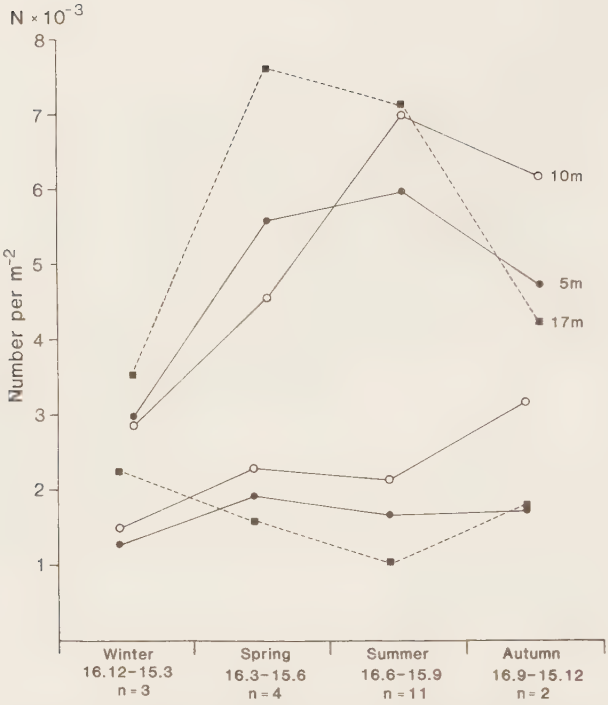

Fig. 7. Mean values of abundance at the three depths in different seasons. In the curves at the bottom of the figure Pygospio elegans is excluded.

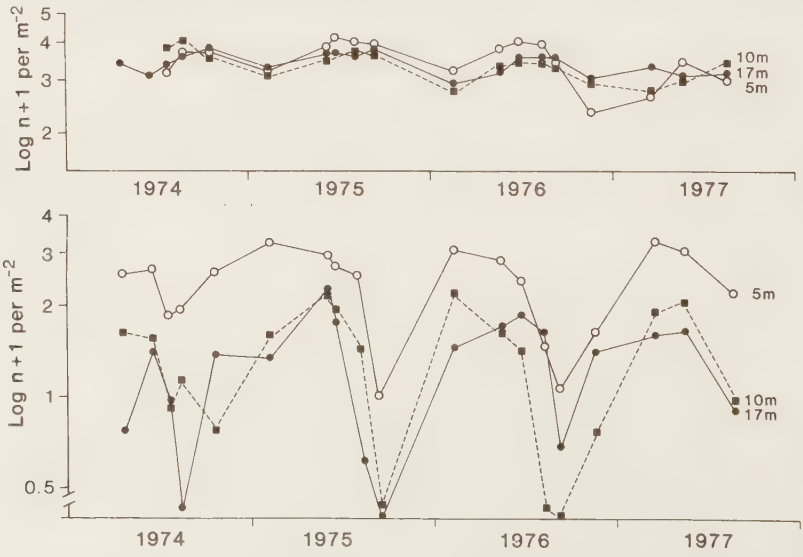

Fig. 8. Temporal change in abundance of Pygospio elegans (a) and Bathyporeia pilosa (b) at the three depths.

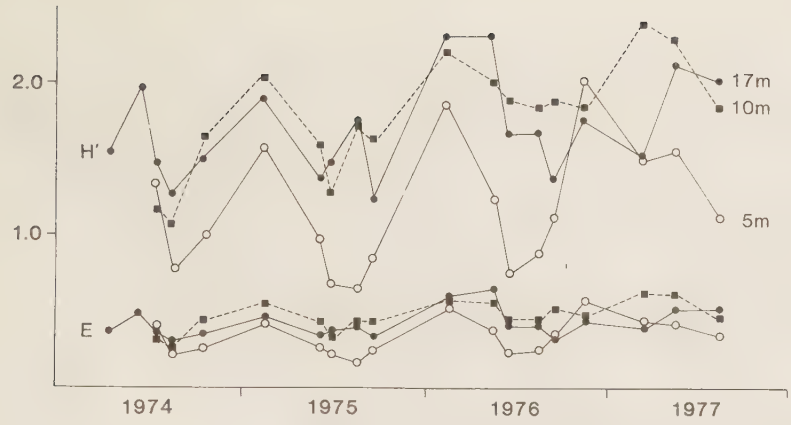

Fig. 9. Temporal variation in diversity, H' and E, at the three depths.

Diversity and similarity

Diversity did not change obviously between years, but a seasonal variation in the H' and E indices was evident at all three depths with low summer and autumn and high winter values (Fig. 9). The difference was statistically significant (Anova, $p < 0.05$) only at the 5 and 10 m depths.

The high community persistence during the four years at the depths investigated is demonstrated in the trellis-diagram in Fig. 10 (P. elegans excluded). At the 5 and 17 m depths the autumn and winter samples from 1976/77, however, showed rather low similarity to other cruises. This was mainly due to increased densities of Hydrobia spp. at 5 m depth and reduced densities at 17 m depth during this period. The number of low similarity values (< 50 %) were higher at 5 m than at 10 and 17 m (57, 23 and 22, respectively). This was partly due to the seasonal variation of the dominant species B. pilosa at 5 m depth.

DISCUSSION

Generally the community structure of the shallow subtidal benthic infauna is reported to be controlled by a combination of abiotic and biotic factors, with the main point in the first group (Clarck & Milne 1955, Lie & Kisker 1970, Field 1971, Massé 1972, Gage 1974, Virnstein 1977). Gage (1974) concluded that in shallow

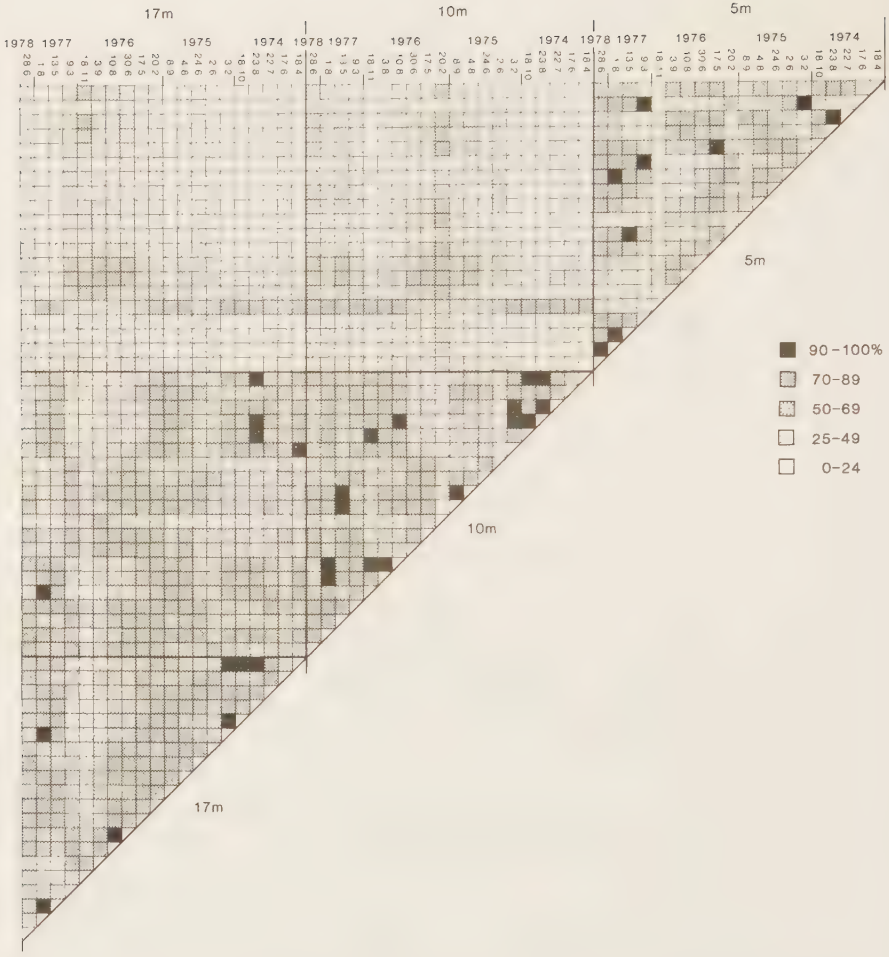

Fig. 10. Trellis diagram showing the similarity within and between stations during the investigation period.

water (< 5 m) the faunal distribution was determined primarily by tidal and wave exposure together with salinity and temperature, whereas in deeper water sediment composition became more important.

Exposure and summer temperature as well as some sediment characteristics differed between the stations investigated by me. Maurer et al. (1979) showed that increasing sediment instability resulted in reduced number of species. In the present study the low number of species at the 5 m depth might be due to increased

exposure. According to Hanson (1978) the wave height rarely exceeds 3 m in the southern Baltic, which affects the bottom sediment to about 6 m depth (Hanson pers. comm.).

The fauna of the Baltic comprises a low number of species. The benthic infauna in the southern Baltic is dominated by members of the North-Atlantic littoral Macoma-balthica-community (Zenkevitch 1963). Some Arctic relicts and Arctic-Boreal species are also found. Of the species with their maximum abundance at 17 m depth, four have an Arctic (Halicryptus spinulosus, Mesidotea entomon, Pontoporeia affinis) or Arctic-Boreal (Harmothoe sarsi) origin (Leppäkoski 1975). Diastylis rathkei is a Low Arctic-Boreal species with winter reproduction, although it occurs in shallow water in more saline areas (Forsman 1938, Rasmussen 1973). The low number of species at the 10 m depth may thus be due to higher summertemperatures, which prevent the Arctic species to establish permanent populations. The migration between deep water (> 40 m) in summer and shallow water in winter reported by Zmudzinski (1967) for four of these five species (except H. spinulosus) was not found in the present study. This may be due to the regular upwelling in the area which does not allow a stable summerthermocline to establish, but favours distribution of the cold-water species.

The four species with maximum density at the 10 m depth are all Atlantic-Boreal species which are restricted to water depths less than 20 m in the Baltic (Persson in press). The reason for their lower density at 5 m depth may be effects of exposure and/or food availability. The density of the juveniles of the molluscs was found to be highest at 5 m depth (Persson 1978).

A preference of marine pelagic larvae to settle in favourable habitats has been suggested by many authors (see Meadows & Campbell 1972, Gray 1974), the bacterial contents of the sediment and the number of adults being decisive factors. In the present study the highest amount of bacteria was at the 10 m depth, which did not fit with the high number of juveniles found at the 5 m depth in an earlier study (Persson 1978). Woodin (1976), however, concluded that successful larval recruitment might be rare in the presence of dense adult assemblages. In this case adult populations of suspension (M. arenaria, C. glaucum) and deposit feeders (M. balthica) may consume or disturb the settling larvae at the 10 and 17 m depths.

Kiørboe (1979) also suggested biological interactions to be

responsible for differential juvenile mortality.

Beukema (1973) reported different optimum locations for juvenile and adult populations of M. balthica, with migration of juveniles (< 5 mm) from shallow water. Such a behaviour would explain the age structure usually found in the Baltic, with high numbers of juveniles in shallow water.

The low biomass found at the 5 m depth indicates more unstable conditions which do not allow the long-lived molluscs to develop a normal population structure with a high number of old individuals. This is contradictory to the theory presented by Jackson (1972), who postulated large infaunal bivalves to be common in intertidal and shallow subtidal sediments due to their ability to burrow deeper and escape the effects of sediment instability. The reason might be that the Baltic species of bivalves are too slow-growing to be able to reach large size between the occurring storms causing catastrophies at the 5 m depth.

A characteristic feature of the community studied was its high persistence demonstrated in the high temporal similarity. Many authors have demonstrated significant changes in softbottom communities between years (Mills 1971, Eagle 1975, Boesch et al. 1976, Buchanan et al. 1978, Larsen 1979). Maurer et al. (1976) found a large variation in species composition through time but stable structure and organization of the community. The high persistence of the benthic shallow water communities in the Baltic may be a consequence of the low number of species, all having a wide distribution. Jackson (1974) suggested that communities with a low diversity and composed by eurytopic species should be evolutionary more stable than communities with a high diversity. The reason should be the low extinction rates of widely distributed species. For those Baltic species which are either mobile or have a pelagic larval stage, such a condition is applicable. Irrespective of season for the disturbance, it is possible to predict the colonizing species.

The seasonal changes in population densities found by me are in accordance with most studies from temperate or cool latitudes (Muus 1967), Boesch 1973, Beukema 1974, Levings 1975, Holland & Polgar 1976, Maurer et al. 1979). They were connected with the reproductive behaviour of all species except Bathyporeia pilosa. The increased density recorded at the 5 m depth in winter for this species was due to seasonal migration from shallower areas (Persson in manus). This migratory behaviour may be the reason

for the reports of large population fluctuations of this species (Löwe 1963).

The distribution pattern of species in the community studied is influenced mainly by two factors viz. exposure (low number of species at 5 m depth) and temperature (increased frequency of Arctic species at 17 m depth). The different size composition of the mollusc populations may be due partly to the negative effect of exposure down to about 5 m depth and partly to the negative influence of adult molluscs on juveniles at increasing depths. The seasonal density variations in the community, repeated each year, may result from biological events as reproduction and migration. The reason for the decrease in abundance in winter is not obvious, but some authors have pointed to predation and spatial competition (Levings 1975, Maurer et al. 1979). Communities with low diversity were claimed to comprise species with a highly predictable appearance (Boesch 1974, Poore & Kudenov 1978), which is confirmed in this study.

The high spatial and seasonal variation in the nearshore community is a complicating factor in pollution studies which are usually made up of only one survey a year. On the other hand the high persistence of the dominant species makes macrozoobenthos a valuable tool at such studies.

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ABUNDANCE AND GROWTH OF A *CARDIUM GLAUCUM* BRUGUIÈRE POPULATION IN HANÖ BIGHT (SOUTHERN BALTIC)

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ABSTRACT

A near-shore population of *Cardium glaucum* was sampled over a period of 18 months, from July 1973 to February 1975, in the Hanö Bight on the eastern coast of Sweden. The year-class of 1972 dominated and recruitment was very low in 1973 and 1974. The reasons for this are discussed. Abundance was slightly higher at 17 m depth than at 10 m, whereas the population at 5 m was very sparse.

The growth was generally faster at 10 m depth than at 17 m. Growth was fastest during June and July. The year-ring was laid down prior to April-June.

INTRODUCTION

Cardium edule L. and *Cardium glaucum* Bruguière have been investigated intensely since 1958, when the differences between the two species were discussed (Petersen, 1958). Most investigations have dealt with these differences (Russel, 1969; Rygg, 1970; Kingston, 1974).

C. glaucum prefers permanent submersion and is intolerant to wave action (Boyden & Russel, 1972). It is very euryhaline and is found in the etangs of the Mediterranean coast (Russel, 1972) as well as in the gulf of Bothnia (Lassig, 1965). However, this euryhalinity has not let to a wide range of any single population. According to Theede & Lassig (1967), *Mytilus edulis* L., *Macoma baltica* L. and *Mya arenaria* L. are more tolerant to sub- and supranormal salinities.

C. glaucum is in the Baltic distributed northwards to the Quark at about 63°N, where the salinity is 4-4.5 ‰ (Lassig, 1965). It prefers shallow water down to about 30 m, which was confirmed by a study in Hanö Bight, where the deepest find was at 20 m. As it is intolerant to wave action, it is found in the upper eulittoral only on sheltered coasts. It seems to prefer sandy bottoms with medium-grained sand, but may be found in other substrates, except black mud

(Petersen, 1958). During the first year it is common in the vegetation, where it climbs by means of byssus threads (Muus, 1967). Jansson (1974) found up to 60 000 ind./m² of *Cardium* spp. in the *Cladophora* belt at Askö during the summer and 50 000 per m² in October. Berg (1973) reported a peak in October with over 2 000 ind./m² at 1-3 m depth. The reason why it occurred in October is probably that he used a 1 mm screen which does not retain juvenile specimens occurring in the summer. Both authors found a very high mortality during the first year.

From SW Finland, Bagge et al. (1965) reported that the maximum abundance in the Lohm area of 93 ind./m² with a biomass (with shells) of 96.8 g/m² was found between 3 and 5 m depth. The high biomass indicates that the population consisted of old animals. In the surroundings of Helsinki, Laakso (1965) only found scattered individuals on sandy bottom. Kosler (1968) found about 100 ind./m² near the Hiddensee island (southern Baltic) at 0.5 m depth.

Studies on production biology have been concentrated on the commercially important *C. edule*, while the ecology, growth and production of *C. glaucum* are less well known. Petersen (1958) gave values from some Danish localities, but no data are available from the Baltic. The aim of this paper is to supply data on the growth of a population in the inner part of the Hanö Bight.

The results were obtained in a benthos study in the Hanö Bight financed by the National Swedish Environmental Protection Board since 1970. I am grateful to Fil. lic. P.H. Enckell for discussions of the manuscript and to Miss Alena Hubalkova for her skilful assistance with the field and laboratory work.

STUDY AREA

The study was done in the inner part of the Hanö Bight along a transect set at right angles to the shore with sampling stations at 5, 10 and 17 m. The three stations are situated at 325, 450 and 650 m from the shore, respectively.

The hydrographical conditions in the Hanö Bight are known to some extent. The salinity is almost constantly about 7.5 ‰. As the coast is facing eastwards, there is a slight up-welling in the summer when westerly winds dominate. This results in low summer temperatures in most years. Since 1971 data have been available from a station "Karlshamn" situated at lat. 56°03'05" N and long. 14°59'00" E (Meddn Havsfiskelab., 1972-74). They show the differences in temperature between 10 and 20 m depth. A thermocline is established during the first half of June and broken up in late September - early October; it is found between the mentioned depths most of this period. Based on 13, 17 and 16 measurements over the years 1972-74 I have calculated the differences in temperature for the six months May-October. Fig. 1 shows that the temperature surplus was highest during 1972 and 1973 for the 10 m depth.

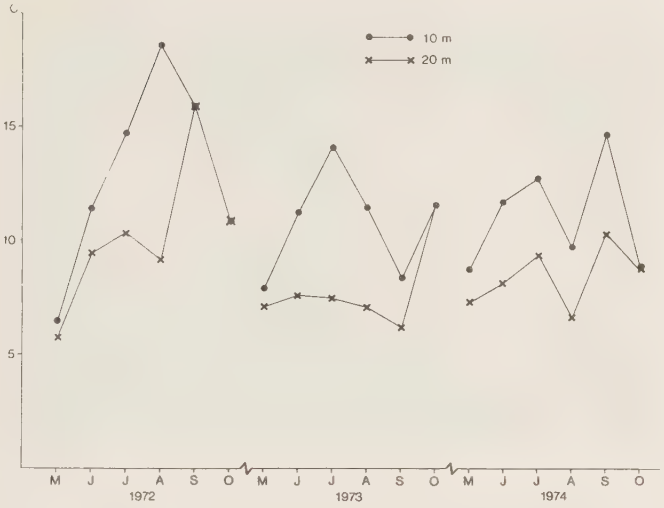

FIG. 1. Monthly mean values of temperatures at 10 and 20 m depths in Hanö Bight during 1972-1974.

Table 1 shows that the sediment is rather uniform along the transect, and that the dominating fractions are fine and very fine sand. Finer particles are only of some importance at 17 m. For the particular sampling date (3 Feb. 1975) the table also shows that the ignition loss was highest for the 17 m sediment, but similar values were found for 10 m samples on other occasions.

TABLE 1. Particle size distribution and ignition loss of sediments taken at three depths along a transect in Hanö Bight on 3 Feb. 1975.

	Per cent at		
	5 m	10 m	17 m
Coarse sand >500 μm	1.2	1.5	0.2
Medium sand 500-200 μm	10.9	18.0	11.3
Fine sand 200-63 μm	87.4	79.6	70.8
Silt and clay <63 μm	0.5	0.9	17.7
Ignition loss	1.1	1.1	2.1

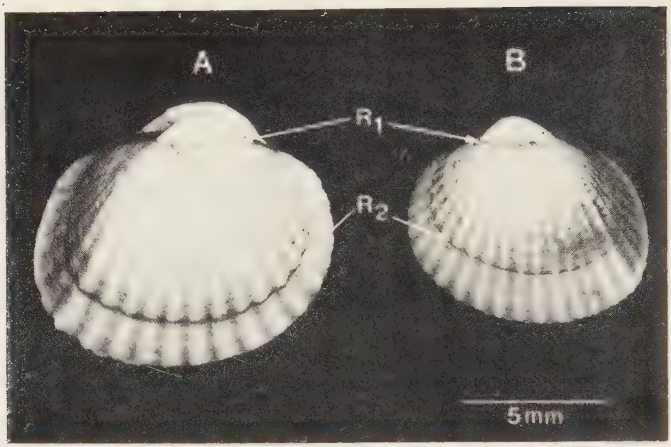

FIG. 2. Shells of *Cardium glaucum* from 10 m (A) and 17 m (B) depths, with two annual growth-rings.

MATERIALS AND METHODS

Between July 1973 and February 1975 the transect was sampled 12 times. Macrobenthos was sampled with a 0.1 m^2 Smith-McIntyre grab, and 10 or 20 replicate samples were taken at each depth. The samples were sieved through a 1 mm stainless steel screen, and the sieve residue was preserved in 4 % neutralized formalin.

Specimen length were measured to the nearest 0.1 mm. As *C. glaucum* has distinct growth rings on the shell the age can be estimated. The length of successive rings were measured, and thus the growth during different years could be calculated (Fig. 2). The difference between the total length on the sampling date and the length of the last ring gave the growth during the growing season.

POPULATION DIFFERENCES WITH RESPECT TO DEPTH

Population density

In the summer of 1973 an abundant population of *C. glaucum* was found at 17 m. Most of the animals were between 3 and 5 mm long and were recruited the preceeding year as they had one year-ring. During 1970-72 few animals were

found, so it meant a highly significant increase. The high abundance in July 1973 was followed by a decrease lasting the rest of the year. In July 1974 there was again an increase to 120 ind./m² (Table 2). Fig. 3 shows that most of the specimens came from the year-class of 1972, and that the recruitment was very low in 1973.

TABLE 2. Abundance of *Cardium glaucum* at three depths along a transect in Hanö Bight.

Sampling date	Number per m² ± SE at 17 m (20 samples)	10 m (10 samples)	5 m (10 samples)
9 July 1973	154 ± 15	–	–
30 Aug. –	10 ± 2	–	–
31 Aug. –	8 ± 2	–	–
22 Oct. –	9 ± 3	72 ± 19	–
28 Dec. –	20 ± 11	–	–
20 Feb. 1974	39 ± 10	–	–
18 Apr. –	90 ± 13	82 ± 18	10 ± 10
17 June –	16 ± 5	34 ± 16	–
22 July –	120 ± 10	34 ± 8	16 ± 11
23 Aug. –	118 ± 13	55 ± 13	2 ± 2
18 Oct. –	56 ± 7	66 ± 6	7 ± 3
3 Feb. 1975	79 ± 10	40 ± 8	11 ± 4

The reason for the low abundance values is not clear. *C. glaucum* is only able to move over short distances (Muus, 1967) and it cannot dig deep enough to avoid the grab. It is possible that the populations are restricted towards greater depths, and as the sampling point may vary by about 50 m (Decca navigation) this could play a role. The population density at 10 m was rather constant, and nothing indicates that the distribution towards the shore should not be continuous.

C. glaucum is said to be a shallow-water species (Muus, 1967), but in the exposed locality of Hanö Bight the abundance is low at 5 m depth, probably because of wave action as the animal is found in the top centimetres of the sand. According to Boyden & Russel (1972) wave action especially affect the larvae at the time of settling.

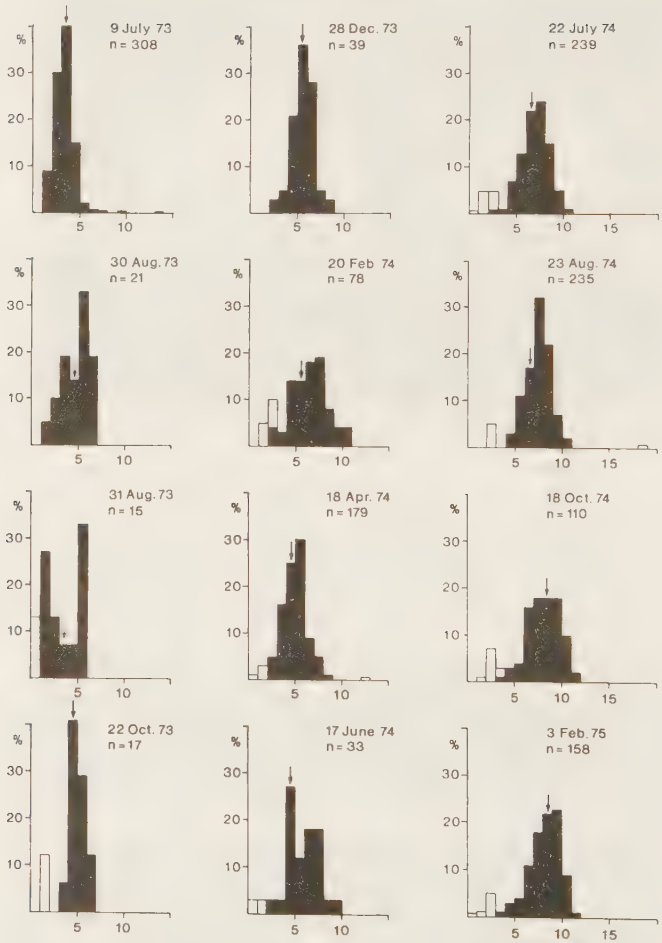

FIG. 3. Size-frequency distribution of *Cardium glaucum* from 17 m depth, Hanö Bight, July 1973 to February 1975. The arrows indicate the mean length of the 1972 year-class (black-shaded area).

Distribution pattern

According to Kosler (1968) *C. glaucum* shows little tendency for aggregation. In my study the tendency for aggregation was strong at 17 m depth with 9 out of 12 sample series indicating aggregation. At 10 m depth only 2 out of 6 series indicated aggregation.

The difference between the two studies is that Kosler used a grab sampling 0.025 m^2, while the Smith-McIntyre grab samples 0.1 m^2. Because of this he got smaller mean values even if the abundance was about the same. As shown by several authors (Clarck & Milne, 1955; Gage & Geekie, 1973; Rosenberg, 1974) demonstration of aggregation depends on sample size.

Growth of the population

Since the 1972 year-class dominated growth could be measured from differences in consecutive ring lengths and from shifts in size-frequency peaks.

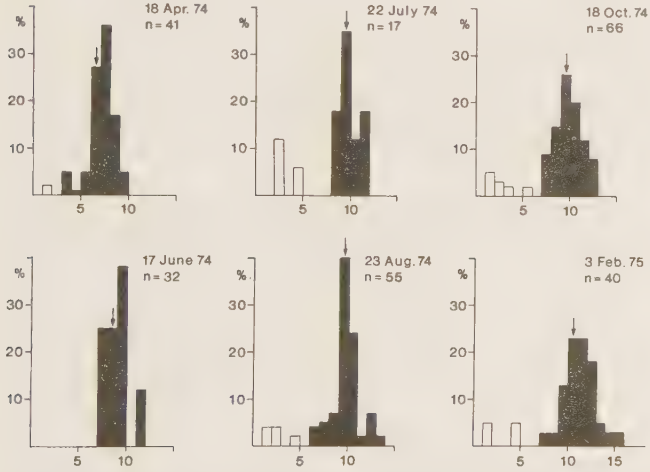

FIG. 4. Size-frequency distribution of *Cardium glaucum* from 10 m depth, Hanö Bight, April 1974 to February 1975. The arrows indicate the mean length of the 1972 year-class (black-shaded area).

If the length of one year-ring (L_t) is plotted against the length of the next (L_{t+1}) the points will give a straight line. This is the Ford-Walford plot (Walford, 1946). The slope of this line gives the rate of change in length increment (K), and the intersection with the 45° line gives the theoretical maximum length, $L\infty$.

As the maximum age was only 3 years the values of the Ford-Walford plot are uncertain. This is because the influence of one successful growth period is great (Hancock, 1969).

The equations for the two subpopulations from 10 m and 17 m, respectively, were estimated by regression analyses.

10 m: $L_{t+1} = 0.5549\ L_t + 6.6882$; $r = 0.790$; $n = 87$. $K = 0.28417$.
17 m: $L_{t+1} = 0.7630\ L_t + 4.0677$; $r = 0.881$; $n = 165$. $K = 0.18915$.

Here r = coefficient of correlation, n = number of specimens, and K = growth constant. Thus growth is fastest at 10 m depth, especially during the first years, whereas the specimens at 17 m continue to grow slowly, but to a greater maximum length. $L\infty$ at 17 m depth becomes 16.7 mm and is a little smaller than the recorded value of 18.9 mm, which was measured for a 9-year old specimen. This has been found for other molluscs, and Johannessen (1973) points out that the Walford graph should be divided in two lines with a steeper slope for the old individuals. The smaller correlation coefficient for the population at 10 m depth is probably an effect of the high growth rate during the second year. $L\infty$ at 10 m depth is 14.9 mm.

The growth differences between the two subpopulations can also be seen in the mean values of growth measured as the differences in length of the year-rings of the populations sampled in February 1975 (Table 3).

TABLE 3. Mean values of growth in mm (± SE) for the 1972 year class of *Cardium glaucum* in Hanö Bight (10 and 17 m depths) and t-tests on the values.

	1972	1973	1974
10 m	3.71 ± 0.13	5.40 ± 0.24	2.28 ± 0.12
17 m	2.86 ± 0.16	3.54 ± 0.10	2.35 ± 0.08
df	91	91	91
t-value	6.240***	8.321***	0.485

The faster growth at 10 m depth is especially obvious during the second year. The increment during the third year is about the same at both depth.

The shift in size-frequency peak is shown in Figs 3 & 4. Most of the specimens from 17 m depth had in July 1973 a length between 3 and 5 mm, which increased

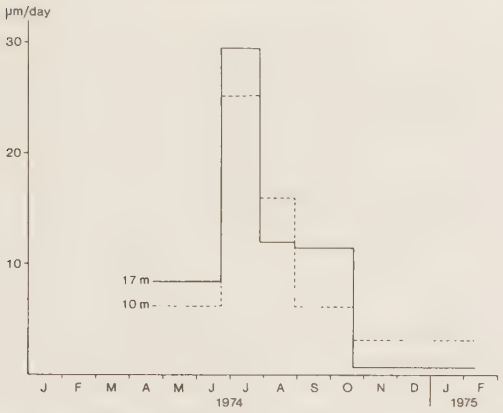

FIG. 5. Length increment in µm/day of *Cardium glaucum* from 10 and 17 m depth, Hanö Bight, during 1974.

to 5-7 mm by December. The same values were found in April 1974 after which they increased to 7-9 mm by July. In February 1975 most of the animals were between 8 and 12 mm long with a maximum length of 11.5 mm.

On animals from 10 m depth measurements were only made for the last six sampling dates. The higher size-frequency peak is clearly seen. In October 1974 it lay between 9 and 11 mm and in February 1975 between 11 and 13 mm, with a maximum value of 16.2 mm.

By measuring the difference between the length of the second year-ring and the length of the animals at the sampling dates between April 1974 and February 1975, detailed studies of growth were made during different periods of the year, (Fig. 5). Growth seems to have occurred during the whole period. Muus (1967) reported that the growth of the 0-group stopped in October, but calculations on his growth-diagram give a length-increment of 2.464 µm/day for the period 8 October to 17 December, which is of the same magnitude as in my investigation. The total length-increment during the year was 2.4 mm at both depths. The highest growth rate was found between the middle of June and the second half of August.

Walton (1919) reported that the year-rings were formed during the winter when growth had stopped. Examination of shells from April showed, however, only slight signs of rings, whereas they were plainly visible in June. This indicates that the year-rings are formed between the second half of April and the first half of June when growth has started again.

DISCUSSION

The fertility of *C. glaucum* is very high. According to Oertzen (1972) the mean number of eggs per gram fresh weight is higher than for *Macoma* and *Astarte* species in the Baltic. This is also seen in the very high abundance of small newly settled juveniles during the summer and autumn reported by Berg (1973) and Jansson (1974). However, the mortality is also very high during the first year so the importance of the adults as food is mostly small in the Baltic.

The population increase at 10 and 17 m depth in the Hanö Bight must partly be due to favourable temperature conditions during the settling period in 1972. Kingston (1974) found that for specimens from southern England the larval growth was inhibited at 10 °C, but after metamorphosis the animals can grow at lower temperatures. Even if the hydrographical situation in the area is not known in detail, one may suppose that the temperature is not the only limiting factor. For a high settlement of spat there probably must be an import from other areas, and so both the temperature and the direction of the current must be suitable. The recruitment during 1973 and 1974 was very low, and only single individuals survived the first year.

The distribution along the transect, with low abundance at 5 m depth, can be seen as an effect of wave-action, but can also be due to a higher predation, as it is known that flounders (*Pleuronectes flesus* L.) feeding on cockles spend the summer in shallow water.

The growth rate is negatively correlated with depth, and thus probably with temperature. This was especially noticeable during the growth period of 1973, when the individuals almost tripled their length at 10 m depth, whereas at 17 m depth it hardly more than doubled. According to the temperature values from the "Karlshamn" station there was a higher mean temperature at 10 m depth during the summer months for all the three years. However, the surplus of 1974 was only about 60 % of that for the two years before. In 1973 the surplus was especially high during the months June and July. From 5 m depth only a few growth data exist, but they indicate that growth is even greater at this depth.

As few values of the growth rate of *C. glaucum* from a similar salinity regime exist, it is difficult to judge whether the locality is normal for the species. Rygg (1970) reported that the length of the 1968-group in April 1969 was between 3.5 and 6.5 mm, which is slightly higher than the 2.8-3.7 mm I found. Henriksson (1967) measured a mean growth of 10 mm during the first year in the Sound, and Petersen (1958) presented growth values of 3-7 mm during the first year in various Danish fjords. He related the differences mainly to the quality and amount of food. Differences in food can be of importance as Muus (1967) reported that the main food of *Cardium* was centric and pennate diatoms suspended in the water, and according to Gargas (1972) the number of benthic diatoms decreases with depth.

The rapid growth at 10 m depth during 1973 is remarkable. Most authors report the same or a slightly lower growth increment during the second and third year.

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SEASONAL MIGRATION OF *BATHYPOREIA PILOSA* LINDSTRÖM IN THE SOUTHERN BALTIC

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ABSTRACT

Quantitative sediment samples were taken between August 1977 through September 1979 at 1 to 5 m depths off eastern Scania, southern Baltic. The infaunal community was almost totally dominated by Bathyporeia pilosa, which was found in densities of 19 000 ind/m^2. In summer and autumn the highest abundance was found at 2-3 m depths whereas the winter and early spring values showed a marked peak at 4-5 m depths. This downshore movement of the population in winter is assumed to be due to a decreased food availability at the shallower depths.

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INTRODUCTION

Species of Bathyporeia are common and often dominating in benthic communities of shallow sandy beaches in North-European marine and estuarine waters (Dahl 1952, Vader 1965, Salvat 1967, Nicolaisen & Kanneworff 1969, Fish & Preece 1970). All the European species prefer fine sand (125-250 µm) and the notation 'Bathyporeia' sand has been used to classify intertidal sand habits (Fincham 1969). Bathyporeia pilosa occupies the highest intertidal zone, and it is the only species penetrating into the Baltic proper where it is found to the Gulf of Finland (Segerstråle 1943). From the Baltic, quantitative data are given by Löwe (1963) indicating high densities (ca 9 000/m^2) at some stations on offshore grounds in the southern Baltic, while Forsman (1956) claimed that B. pilosa was not one of the more common amphipods of the Baltic.

In a study of temporal changes in community structure along a downshore transect in the Hanö Bight (Persson in manus), B. pilosa varied considerably in abundance at 5 m depth, with high densities in late winter and early spring. At 10 and 17 m depth density was low and this pattern of variation was only rarely met with. Thus, it was presumed that the variations in abundance at 5 m were due to migration between the 5 m depth and shallower areas.

Studies of migration in Crustacea suggest that temperature-salinity effects regulate the habitat selection during the ontho-

genesis (Dorgelo 1975, Baker 1978). These factors were primarily used in this study to evaluate the migration pattern of Bathyporeia pilosa in the Hanö Bight.

STUDY AREA

The transect investigated was at the eastern coast of Scania in the Hanö Bight, southern Baltic. This part of the coast is very exposed by Baltic standard. The slope of the transect is rather gentle (1/60) and the substrate consists of well sorted sand with fine sand as dominating fraction (median particlediameter = 220 µm). In connection with storms, however, the finest particles are washed away from the shallow areas (< 2 m) and medium sand becomes dominant (275 µm). The organic content measured as ignition loss (550° C) is constantly below 1.0 %.

Salinity varies only slightly around 7.5 o/oo, with lower values connected with ice-melting in spring and higher values with up--welling of deep water. Mean seasonal temperature in the southern Baltic ranges between 2.2° C in March and 16.3 in July (Matthäus 1977). Occasionally, however, winter temperatures below zero were measured (Fig. 1). In summer a thermocline establish at 15-25 m depth, but in winter the water is homoitherm to about 40 m depth (Matthäus 1977).

The associated macrobenthic community is represented by an impoverished Macoma balthica-community (Persson in manus) at the 4 and 5 m depths, but in shallower areas the only additional species found was Eurydice pulchra Leach (Crustacea, Isopoda). In summer, dense populations of Sandeel (Ammodytes lancea Yarell) and Brown Shrimp (Crangon crangon (L.)) are found along the transect together with juveniles of Flounder (Platichtys flesus L.) (Sasdy 1972).

MATERIALS AND METHODS

Sampling was performed at every m between 1 and 5 m depth in the period August 1977 through September 1979. Eight replicates were taken at each depth with a 28 cm^2 core sampler working to a depth of 8 cm in the sediment. Sediment samples for particle analyses were collected from the last sample at each depth. Temperature

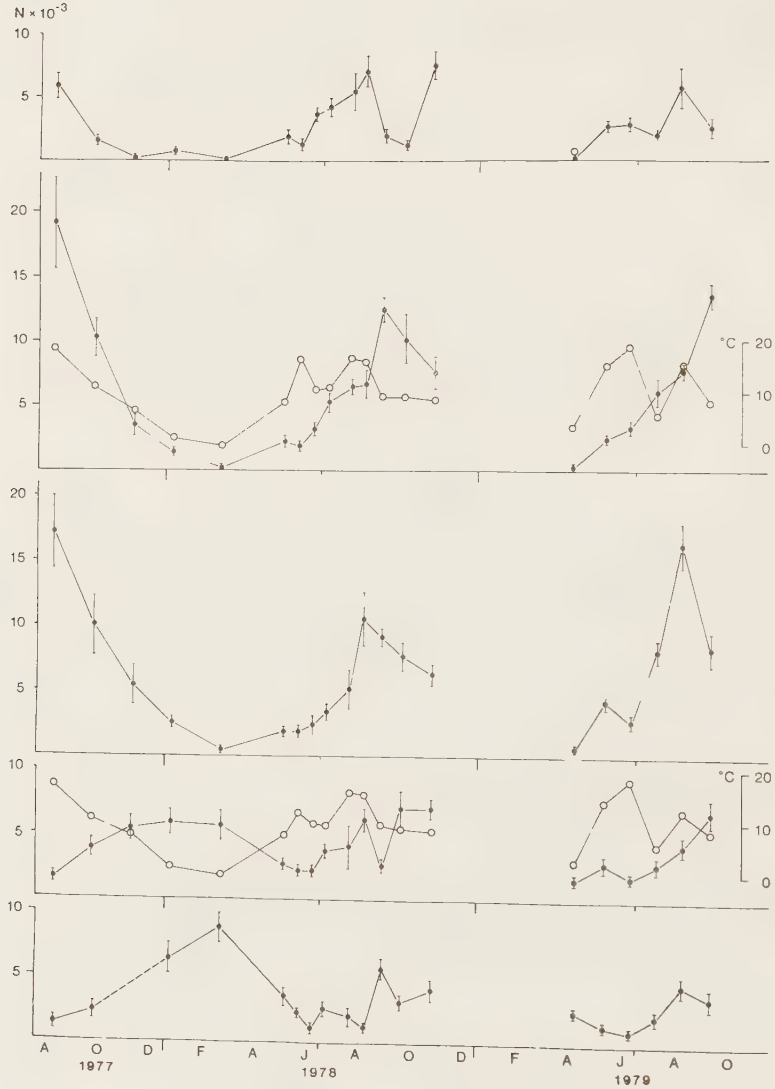

Fig. 1. Population density of Bathyporeia pilosa at 1 to 5 m depths between August 1977 and September 1979. Bottom temperatures at 2 and 4 m depths are included. Vertical bars denote Standard error.

was measured with a reversing thermometer at 1 and 4 m depth. Water-samples were taken at the surface and the 4 m depth and the salinity was measured with a wheatstone bridge.

The samples were sieved through a 250 mm sieve and preserved in 80 % alcohol. The numbers of the macrobenthic species were counted. Individuals of Bathyporeia were divided in adults and juveniles. Adults (> 3 mm) were sexed, and both sexes divided in two stages viz. females with and without egg or embryoa in the brood pouch and males with or without the flagellum of the antenna longer than half the body length. In 1978 the length of the individuals was measured from the tip of the rostrum to the end of the telson.

RESULTS

ABUNDANCE AND SEASONAL VARIATION

The highest density was found at 2 and 3 m depths in August or September, maximum value 19,120 ind./m^2. At the three other depths investigated the highest densities were below 9,000 ind./m^2 (Fig. 1). Only one of the 99 station values was a zero value, viz. 1 m in April 1979.

There were clear seasonal changes in population density (Fig. 1). This pattern can be separated in two sections. The populations at 1-3 m depths have a marked peak in abundance in August--September, and a minimum in March-April, whereas the populations at 4-5 m depths have the peak in October-March and the minimum in summer, In November and June the density is about the same at all depths.

The total number of individuals present along the transect (325 m) was highest in August every year and lowest in May (1978) or April (1979). The summer values were about one magnitude higher than the spring values.

REPRODUCTIVE PATTERN AND GROWTH

There were no detectable differences in reproductive pattern between different depths during the period studied. Therefore, only the cumulated values for the 1-5 m depths are represented in Figs 2 and 3.

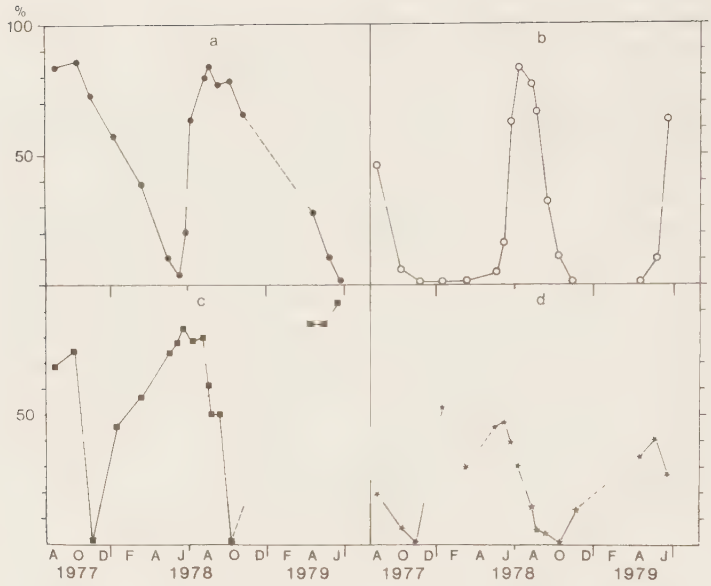

Fig. 2. Population structure of the B. pilosa population at 1 to 5 m depths, August 1977 through June 1979.
a/ Frequency of juveniles (< 3 mm) in the population.
b/ Frequency of gravid females as a percentage of the total female population.
c/ Frequency of mature males as a percentage of the total male population.
d/ Sex ratios of males to females.

Gravid females were found from the beginning of March to the beginning of October. High frequencies of gravid females were, however, recorded from late June through August (45-83 % of females gravid) (Fig. 2). Males with prolonged antennae appeared already in January. The highest number of mature males was found in June. The males disappeared in October after a decline in August. This can be seen from the decreasing sex ratio in the autumn. Sex ratios of males to females ranged from 0 : 1 to 0.53 : 1.

The number of juveniles (< 3 mm) decreased during spring and had a minimum in late May and early June. Then the recruitment of the new generation started and a maximum of juveniles occurred in August through October.

The size frequency distribution in Fig. 3 shows that Bathyporiea pilosa in the Baltic has one generation a year only. In winter, the growth is slow and in late May and early June almost all the individuals have entered the adult stage. In June recruitment of juveniles starts. A first maximum in early June com-

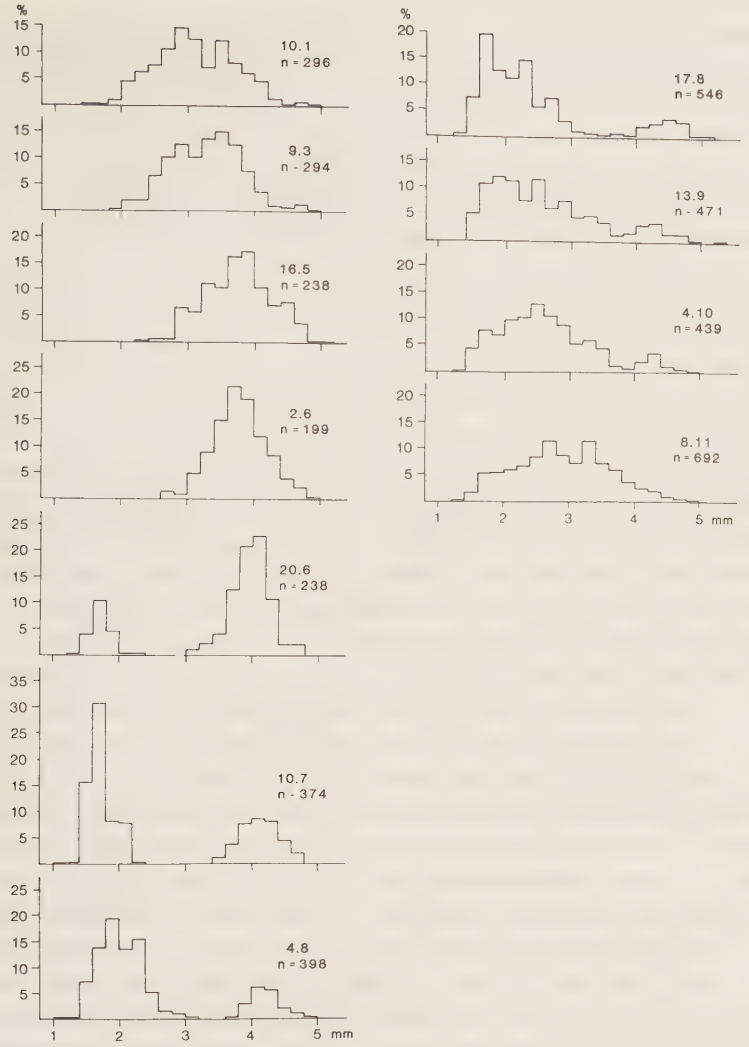

Fig. 3. Length-frequency histograms (0.2 mm length groups) for the B. pilosa population, 1-5 m depth, in 1978.

prises individuals of 1.6 - 1.8 mm. A second maximum in the second half of August indicates that many females produce a second brood. In October the last individuals of the winter generation disappear.

The seasonal variation in the zonation of the Bathyporeia pilosa population investigated intimates a well-developed migration pattern. The main part of the population is moving offshore in winter and inshore in late spring and early summer. Such a pattern is the most common type in Crustacea according to Dorgelo (1975). Movements in the reversed directions are found e.g. in the Baltic glacial relicts (Zmudzinski 1969).

The vertical seasonal migrations in Crustacea have been connected with reproductive patterns or temperature and/or salinity reactions. As salinity is almost stable in the area studied, this factor is ruled out.

Fish & Fish (1978) showed that horisontal migration of Bathyporeia pelagica (Bate) into an estuary in winter enabled the species to extend its breeding season. Wooldridge (1981) found an intraspecific zonation in the mysid Gastrosaccus psammodytes Tattersall, with gravid females moving inshore to escape excessive turbulence and sediment instability. In my study no difference could be found in the reproductive pattern at different depths, and thus onthogenetic factors should not be an explanation to the migration.

The univoltine life cycle of B. pilosa in the Hanö Bight differs from the descriptions by Movaghar (1964), Salvat (1967), Fish & Preece (1970) and Jazdzewski (1970) who found a bivoltine lifecycle with the spring generation breeding already in summer. The slower growth in the Hanö Bight might be explained by the influence of lower temperatures (see Fish 1975) or food limitation due to the high population densities. The highest density found in the studies mentioned above was 4,600 ind/m^2 (Movaghar 1964).

In intertidal populations of Bathyporeia pilosa in France and Great Britain a movement downshore in summer has been recorded (Salvat 1967), Fish & Preece 1970, Ladle 1975). This was related to harsh environmental conditions (high temperatures) at high beach levels. According to Salvat (op. cit.) the vertical distribution was lowered with 1 m in July compared to January. Similarly, Sameoto (1969) recorded migration into the intertidal zone in summer from sublittoral areas of two species of Bathyporeia due to the rize of the temperature. The migration pattern of B. pilosa in the Hanö Bight at first seems to fit into the conventional theory 'moving towards warmer water' (Kinne 1970, Baker 1978). However, the temperature data contradict this, primarily because of equally low winter temperatures (min. -0.3° C) at 2

and 4 m depths. According to Matthäus (1977) the Baltic water is homoitherm to 40 m depth in winter.

Dexter (1971) suggested another factor to explain the downshore movement of Neohaustorius schmitzi Bousfield in autumn, viz. increased wave action in combination with low sand temperatures. In the Baltic heavy wave action may be expected in October -November and March-April. However, B. pilosa is well adapted to exposed unstable sediments due to its excellent swimming and digging ability (Nicolaisen & Kanneworff 1969). Increased activity at periods of sediment instability, however, results in increased metabolic rate and must be compensated by increased food consumption. B. pilosa feeds on sessile microbenthic diatoms and detritus (Nicolaisen & Kanneworff op.cit., Dahl 1973). No measurements of microbenthic primary production were made in this study, but literature data show a seasonal variation with high values in the period June-November (Gargas 1972, Cadée & Hegeman 1974, Sundbäck 1979). There is a similar seasonal pattern in migration of the Bathyporeia pilosa population and the microbenthic primary production and this agreement might indicate that migration is induced by food limitation in shallow water. Hildebrand (1974) found a correlation between drift and food levels in freshwater streams and suggested that high levels of intraspecific competition for food increased drift. Grant (1980) hypothesized food availability to be a complementary factor to induce drift by tidal currents in haustoriid populations. The relatively high population densities of B. pilosa in winter at 4-5 m depths may be explained by lower energy consumption due to increased sediment stability and higher amounts of detritus.

The dense populations of Bathyporeia pilosa at exposed unstable sediments in the Baltic are exploited by at least three species of predators. Sasdy (1972) reported that B. pilosa was the most important food item of 1-3 year old individuals of flounder in summer. Stomach analyzes of sandeels showed B. pilosa to be the second most important food item after copepods (Persson unpublished). According to Plagmann (1939) the brown shrimp mainly captured these amphipods in shallow water in the German Bight.

In conclusion, temperature and salinity are not the decisive factors controlling the migration pattern of Bathyporeia pilosa. Instead a combination of food availability and sediment instability seems to be the critical factor. Due to its great swimming and digging capacity B. pilosa can resist the rigorous and chang-

ing environment in shallow water, but when food availability decreases in late autumn the main part of the population has to move to more sheltered depths.

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The effect of microbenthic grazing by an amphipod, Bathyporeia pilosa, Lindström

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Introduction

Bathyporeia pilosa, a dominating member of the macrofauna in shallow, exposed sand bottoms in the Öresund (The Sound), lives off the microflora of the sand grains (NICOLAISEN and KANNEWORFF 1969). Our purpose was to investigate a possible relationship between *B. pilosa* and microbenthic algae and to study food selectivity in *B. pilosa*.

Material and methods

The uppermost layer (1 cm) of sand and specimens of *Bathyporeia pilosa* were collected from a moderately exposed bottom (depth 0.5 m, salinity ca. 10‰)in the central part of the Öresund. We introduced different densities of *B. pilosa* (0–214) into plexiglass cylinders (area 80 cm^2) with washed sand (to remove non-sessile organisms) and filtered seawater. The cylinders were incubated in the laboratory and exposed to daylight. Range of temperature was 16–18° C. Chlorophyll a content (LORENZEN 1967) and primary production (^{14}C-uptake, GRÖNTVED 1960) were measured in the top 5 mm of sand once a week. Two experiments were conducted: December-January, 1979–80 (A), and May-June, 1980 (B).

To study the composition of the diatom species in the sand, stomach contents and faecal pellets we prepared permanent microscope slides. 500 diatom frustules per slide were identified and counted. The relative abundance was expressed as percentage occurrence. Selectivity was determined using IVLEV's (1961) electivity coefficient. This index ranges from -1 to $+1$.

Results and discussion

The two experiments showed the same general tendency, i.e. increased chlorophyll a content and primary production with decreasing numbers of *Bathyporeia pilosa* (Fig. 1). This tendency became evident after one week in Experiment A, and after three weeks in Experiment B. Thus the microbenthic flora seems to be limited by grazing by *B. pilosa*.

Our results are mainly in accordance with those of BRANCH and BRANCH (1980), NICOTRI (1977) and PACE et al. (1979). However, in Experiment B the highest increase in primary production occurred with the lowest animal density i.e. 1/4 of the density at the sampling site. PACE et al. (ibid.) also found that a low level of grazing stimulated the microflora, whereas HARGRAVE (1970), COOPER (1973) and others found that natural densities of grazers enhanced the primary production of the benthic microflora.

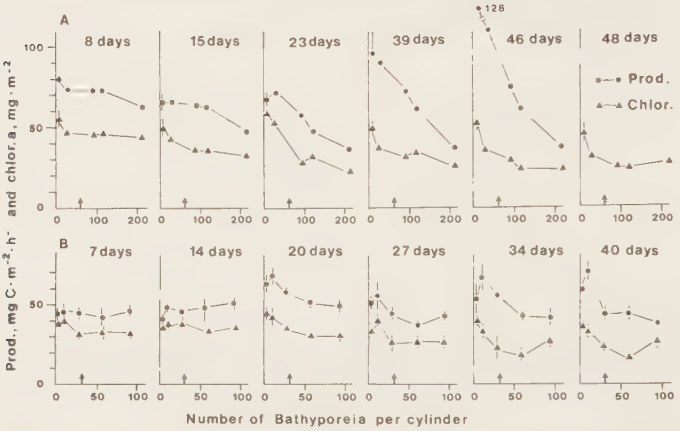

Figure 1

The effect of varying densities of *Bathyporeia pilosa* on the primary production and chlorophyll a content of the microbenthic flora in the two experiments. Bars show the range of two parallels. Arrows show the density of *B. pilosa* at the sampling site.

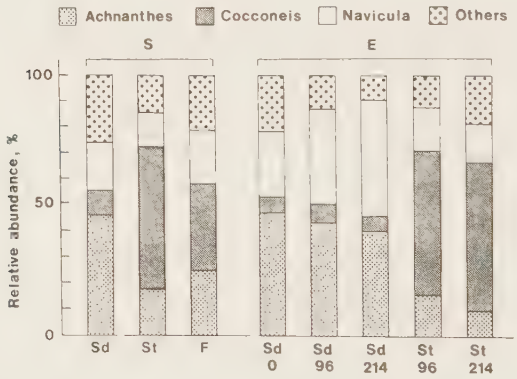

Figure 2

The relative abundance of the three commonest diatom genera in the sand (Sd) and in the stomach contents (St) and faecal pellets (F) of *Bathyporeia pilosa*. S represents conditions at the sampling site (December, 1979) and E conditions at the end of Experiment A. Figures show the animal densities per cylinder.

The microflora of the sand was dominated by small pennate diatoms (mean cell length 10 μm) such as *Achnanthes hauckiana* Grun., *A. lemmermannii* Hust. and *Navicula* spp. from the group Naviculae lineolatae. Altogether approx. 60 species were identified.

In Experiment A about half of the microflora ingested by *Bathyporeia pilosa* were *Cocconeis* spp., in particular *C. scutellum* Ehr. (Fig. 2). The electivity coefficient was 0.64–0.84 based on relative abundance. NICOTRI (1977) suggests that passive selection by diatom grazers results from differences in the morphology and accessibility of the species. McELHONE (1980), working with oligochaetes, found a positive correlation between ingestion and large cell volume. The large numbers of *Cocconeis* spp. ingested by *B. pilosa* in Experiment A could be explained both by the size (mean cell length 20 μm) and by the location on the sand grains. As *Cocconeis* spp. attach themselves firmly to the surface of the sand grain they are often found in exposed positions thus being more accessible than species found in the cavities of the sand grain.

The reason for lack of selectivity in Experiment B may be the lower relative abundance (4 % as against 9 %) and the smaller size (12 μm as against 20 μm) of *Cocconeis* spp. in the sand.

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Long-term changes in population density of Diastylis rathkei, Krøyer (Cumacea) in different depths in the Hanö Bay, Southern Baltic

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Abstract

Grab samples were taken at seven stations (10–58 m) in the Hanö bay in July-August during the period 1970–78. A high percentage, 26 – 60 %, of surviving adults (females) were found. At stations shallower than 38 m increasing population densities of *Diastylis rathkei* were found until 1975 after which they decreased again. The population increase was found to be positively correlated to high water temperature during the previous winter. At 43 m depth the population changes were numerically small. Variations in the oxygen regime in the Bornholm basin caused the population changes at 58 m depth.

Introduction

Diastylis rathkei is an important member of the benthic fauna of the southern and western Baltic. In the latter area it has been found to constitute a major food item to demersal fishes such as the dab (*Limanda limanda*), cod (*Gadus morhua*) and flounder (*Platichthys flesus*), (ARNTZ 1971, 1974 and 1977). According to MULICKI (1957) it is a coldwater species inhabiting waters deeper than 40 m in the southern Baltic. The limiting abiotic factors were suggested to be temperature ($>$ 12° C) and salinity ($<$ 7.5 ‰). The population on the west coast of Sweden, however, has been found to tolerate higher temperatures ($\sim$ 19° C) (FORSMAN 1938).

In spite of the importance of *D. rathkei* as a link between the benthic and pelagic system its ecology is hardly known. Its life history has been investigated by FORSMAN (1938), KRÜGER (1940) and VALENTIN and ANGER (1977). With the exception of the extensive study of DEMEL and MULICKI (1954) only a few occasional data on abundance in the southern Baltic are reported during the last 60 years. The reproduction period starts in October, and most of the young leave the marsupium between January and April. The species normally has a life-span of one year, but a small number of females survive for two to three years. Changes in population density of *D. rathkei* between years have been correlated with either low winter temperatures (FORSMAN 1938), or changes in predation pressure by demersal fishes (VALENTIN and ANGER 1977).

The value of long-term studies of benthic communities when trying to understand the dynamics of marine ecosystems is stressed e.g. by MILLS (1975). However, such long-term studies are nevertheless scarce. The aim of this paper is to evaluate the temporal and spatial population changes of *D. rathkei* over a period of eight years.

Material and methods

Quantitative samples were taken with a 0.1 m² Smith-McIntyre grab and sieved through a 1.0 mm sieve. Five, ten or twenty samples were taken at each station. The sieve residues were preserved in 4 % neutralized formalin. Sediment was taken from the last sample and in 1970 analysed by dry sieving for particles > 63 μ and by sedimentation for particles < 63 μ. The amount of organic content in the sediment was measured every year as ignition loss at 550°C for three hours. All the species were sorted out and counted. The material of *D. rathkei* was measured for total length, from the fore end of the pseudorostrum to the tip of the telson. Mean surface temperatures for the two periods January-March and July-September were calculated from data given twice a week by the Swedish Meterological Institute. Information about fishery yield in the southern Baltic was found in the Swedish statistical year-book.

Study area

Seven stations were sampled in the Hanö bay at depths between 10 and 58 m (Fig. 1). Samples were taken in July or at the beginning of August every year. In the calculations stations 1–3 and 4–5 were put together. The six stations between 10 and 43 m depth had sediments of fine to coarse sand with a slight increase in silt content with depth (Table 1). The organic content was low and rather constant. The station at 58 m had a muddy sediment with rather high organic content.

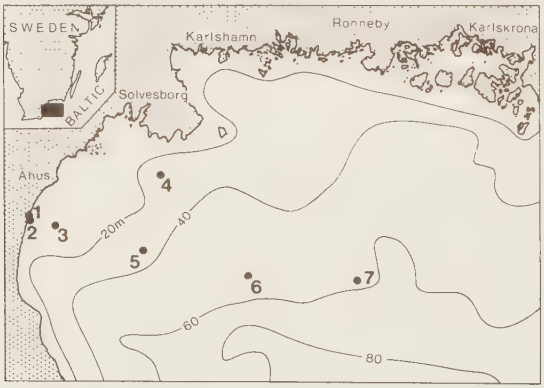

Figure 1

The study area with the sampling stations indicated

During the summer a thermocline is established at depths of 15–20 m with temperatures usually above 15° C. In the western part of the bay this thermocline is sometimes disrupted due to upwelling, which may give summer temperatures in the surface water below 8° C. When the thermocline breaks down in the autumn, usually in September, the temperature of the layer between 20–35 m is somewhat increased and may in some years reach 10–12° C (HERNROTH and ACKEFORS 1979). The salinity of

Table 1

Depth and sediment data for the seven Hanö bay stations sampled

Station	Depth (m)	Mdø	Mean particle size	Ignit. loss (%)
1	10	2.12	0.230 mm	1.10 ± 0.11
2	17	2.42	0.187 mm	0.94 ± 0.09
3	14	1.68	0.312 mm	0.32 ± 0.05
4	25	1.67	0.315 mm	0.74 ± 0.17
5	38	1.32	0.400 mm	0.85 ± 0.11
6	43	2.17	0.222 mm	1.05 ± 0.14
7	58	5.11	0.029 mm	6.49 ± 0.28

the upper 30 m is mostly between 7.0 and 8.0 ‰, with the lowest values in the nearshore area. Between 30 m and the primary halocline at 50–60 m there is a gradual increase in salinity by about 2 ‰.

The water mass down to 60 m depth is usually fully saturated with oxygen. In deeper waters the oxygen content varies due to the dynamics of stagnation and inflow of salt water from the Kattegat. The bottom area between 50–60 m is only seldom reached by the stagnating water, but when new and heavier water flows in the old bottom water is lifted up and may cause damage to the benthic fauna at these depths.

Phytoplankton primary production is rather high in the Hanö bay and amounts to about 120 gC/m²/year, (LINDAHL 1977). A spring bloom is normally found in April where diatoms dominate.

Results and discussion

The length measurements showed that the population in summer was composed of both juveniles from last winter (0) and adults from the year before (1 +) at stations down to 38 m depth, (Fig. 2). At the two deepest stations there were indications of individuals being two years old (2 +). The mean length of juveniles was about 4–5 mm, of 1 + animals 8–10 mm and of 2 + animals 12–14 mm. The share of surviving adults varied between 26 and 60 % of the total population, with the greatest variation in the 25–38 m interval. There was no correlation between the number of surviving adults and the population size of the next year.

The high number of surviving adults (females) is not in accordance with the results presented by VALENTIN and ANGER (1977) from the Kiel Bay. They found only 2–3 % of survivers from the preceding year at the beginning of August. It is also in contradiction to the assumption of KRÜGER (1940) of earlier disappearing of the 1 + animals in the eastern part of the Baltic.

The population changes of *D. rathkei* in the area studied can be divided into four fractions depending on depth and temporal variations.

In shallow water, 10–17 m, represented by three stations, the population density was very low in the first three years, mean 6 ind/m² (Fig. 3). In the next two years the density increased and was then followed by a heavy peak in 1975–76 with a mean of 117 ind/m². During the last two years of the investigation the population again showed low abundance, mean 6 ind/m².

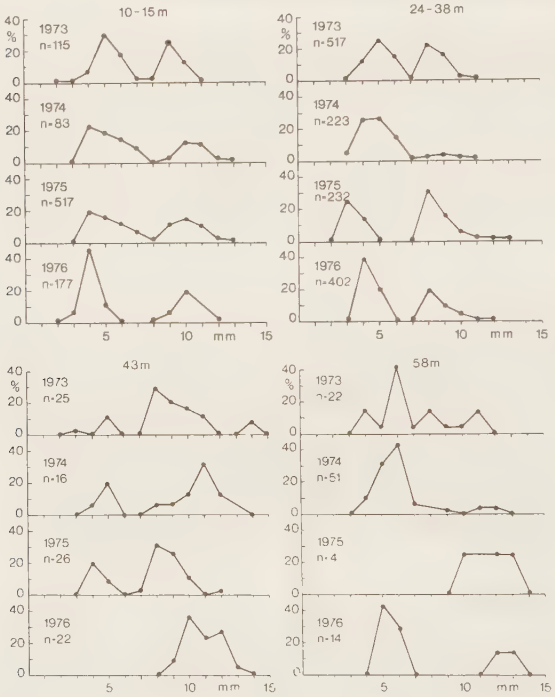

Figure 2

Length frequency distribution of *Diastylis rathkei* at different depths in 1973–1976

The population changes at the two stations at 25 and 38 m depth followed the same general pattern, although the mean levels were higher and the maximum values not so outstanding.

At 43 m depth the population changes were numerically small with a range of 12–44 ind/m², and with no obvious pattern.

The population at 58 m showed very great between year fluctuations. Thus maximum densities of about 100 ind/m² were recorded every third year. Very low values, 10–20 ind/m², were noted in the four years between these peaks.

Correlation analyses of these population changes in different depths in relation to abiotic as well as biotic factors were carried out using Spearman's rank correlation method (Table 2). Positive significant correlations were found between high surface

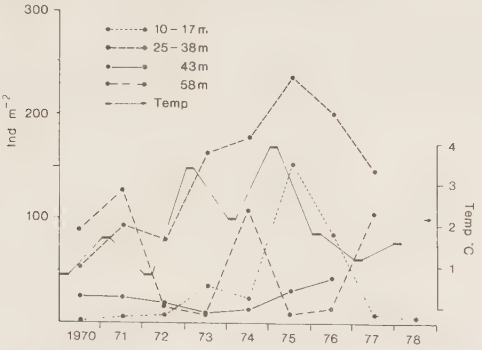

Figure 3

Variations in abundance of *Diastylis rathkei* at four different depths. Inserted values of temperature represent mean surface temperatures for the three months January-March, arrow indicates long-term mean of winter temperature in surface water

Table 2

Evaluation of population changes of *D. rathkei* in the period 1970–78 in four depths. Statistically significant correlations are shown by* ($p < 0.05$), Spearman's rank correlation

Parameter	Depths m			
	10–17 m	25–38 m	43 m	58 m
I	0.80*9	0.88*8	– 0.14 7	– 0.48 8
II	0.22 "	0.36 "	– 0.17 "	– 0.45 "
III	– 0.40 4	0.20 4	0.40 4	0.80 4
IV	0.10 9	– 0.29 8	– 0.12 7	– 0.14 8
V	– 0.03 "	– 0.45 "	0,02 "	0.07 "
VI	– 0.03 "	– 0.16 "	– 0.04 "	0.83*"
VII	– 0.30 "	– 0.45 "	0.76 "	0.60 "
VIII	0.22 "	0.55 "	– 0.51 "	–

I = Mean surface temp. Jan.–March v. *D. rathkei* population in summer
II = Mean surface temp. July–Sept. v. *D. rathkei* population next summer
III = Primary prod. Jan.–March v. *D. rathkei* population in summer
IV = Swedish yield of cod in southern Baltic v. *D. rathkei* population the year before
V = Swedish yield of flat-fish in south. Baltic v. *D. rathkei* population the year before
VI = Population density of *Pontoporeia* spp. v. *D. rathkei* population
VII = Population density of *Harmothoe sarsi* v. *D. rathkei* population
VIII = Population density of *Saduria entomon* v. *D. rathkei* population

temperatures in January-March and high population size in the following summer in the two shallowest depth intervals, and likewise a positive correlation between population size of *D. rathkei* and *Pontoporeia femorata* at 58 m depth.

In Fig. 3 the temperature values are inserted together with the abundance values. The mean value is approximately calculated from data in MATTHÄUS (1977). The use of surface temperatures in assessing changes in benthic populations is supported by the fact that in winter the water is homoiotherm to about 40 m depth (MATTHÄUS 1977)

The impact of winter temperature on benthic populations has recently been demonstrated. According to BEUKEMA et al. (1978) and BUCHANAN et al. (1978) the mild winters between 1972–77 changed the community composition in the investigated areas of the North Sea. BODDEKE (1978) showed the stock of *Crangon crangon* to have a positive correlation to low winter temperatures. In certain years, however, no correlation was found, and this was argued to be caused by increased predation pressure by juvenile cod.

The effect of low winter temperature on *D. rathkei* may be direct, as proposed by FORSMAN (1938), who found that moulting was obstructed. It is, however, also possible that the effect is indirect through other parameters influenced by temperature. Low winter temperature may delay the start of the phytoplankton spring bloom. ACKEFORS and LINDAHL (1975) stated that this does not start until temperature exceeds 2.5° C. The zooplankton population is low at this season and consequently most of the spring bloom reaches the bottom in a few weeks (HERNROTH and ACKEFORS 1979). Very little is known about the diet of *D. rathkei*, but according to FORSMAN (1938) the species is a detritus feeder. Preliminary examination of stomach contents gave diatoms and unidentifiable material.

ELMGREN (1978) suggested that the growth of the *Pontoporeia* populations of the northern Baltic is correlated to the height of the spring bloom, and thus food limited. In my study there were no similarities in the population changes of *D. rathkei* and *Pontoporeia affinis* at shallow depth (10–43 m). Thus the results give no support to the idea of food limitation as a cause for between-year fluctuations of these species in this part of the Baltic. Furthermore the abundance values of both species are usually much lower than those of *Pontoporeia affinis* + *femorata* in the northern Baltic.

VALENTIN and ANGER (1977) suggested that high abundance of *D. rathkei* in 1968 and 1974 compared to values during the period 1925–60 was due to decreased predation by demersal fishes. In my study, however, no correlation was found either with the two invertebrate predators *Harmothoe sarsi* and *Saduria entomon* or the yield of cod or flatfishes. This lack of correlation between yield of demersal fish and population density of *D. rathkei* does not necessarily mean that their impact on *Diastylis* is small. The available data on yield of fish are somewhat crude and include a larger area including the Hanö bay. A better estimate of predation pressure by cod would be the strength of the different year-classes. THUROW (1974) reported a difference in numbers of up to 15 times between good and bad years. According to ARNTZ (1974) *D. rathkei* is the most important food for young cod. It is, however, possible that the importance of *D. rathkei* to demersal fishes is less in the Hanö bay than in the western Baltic due to the presence of *Saduria entomon*. This species is, according to HESSLE (1923), the main food item for cod and dab in the Baltic proper. Furthermore the preference of cod for *D. rathkei* did not become clearly evident before the biomass reached about 3 g/m² (ARNTZ 1974), and the maximum values in my study were about 1.8 g/m².

The population changes at 58 m were closely connected to the oxygen regime in the deep water both for *D. rathkei* and *Pontoporeia femorata*. Inflow of new water took place in 1972 and 1973 and caused the low population values (Fig. 4). In 1974 no new water came in, but the oxygen values decreased in the deep water until winter 1976. This made the oxygen values very low even at 60 m already in 1975 (saturation values of 5 % were found, ANON 1977) and may explain the low densities at station 7. In 1977 a new inflow of water took place after the sampling period.

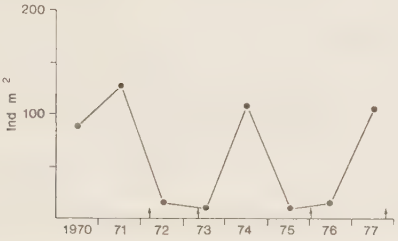

Figure 4

Variations in abundance of *Diastylis rathkei* at 58 m depth. Arrows indicate inflow of salt water from the Kattegat

The correlation between the winter temperature and the abundance of *D. rathkei* in the following summer leads to a modification of the theory proposed by MULICKI (1957) that high summer temperatures together with low salinities limit the occurrence of the species in shallow water in the southern Baltic. In the western Baltic and on the Swedish west coast is appears in shallow water, e.g. abundance values of 3 500 ind/m² were found in the Laholm bay at 10 m depth in summer (SJÖBLOM unpublished). The major limiting factor in the southern Baltic seems to be low winter temperature.

The results of this study emphasize furthermore two general points. For investigations of population dynamics long-term data are necessary for generalizations about population changes and species relations, and if you get long-term data for the biota, they should be supplemented by relevant abiotic parameters. This would also facilitate the attempts to make predictions, which should be the ultimate aim of our work.

Acknowledgements

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MACROBENTHIC ASSOCIATIONS OF THE HANÖ BIGHT, SOUTHERN BALTIC

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ABSTRACT

In August 1975 a stratified random sampling programme at 46 stations was performed. The highest number of species, 21, was found in shallow water (5-19 m), whereas the highest biomass, 132,04 g/m^2, was found between 20-29 m depth. Diastylis rathkei (Crustacea; Cumacea) and Macoma balthica (Mollusca; Bivalvia) showed the widest distribution and were found at 37 and 36 stations, respectively. Community analyses were made by both qualitative and quantitative methods, which yielded six and seven associations, respectively. The species found could be divided in three groups with different depth distribution correlated with hydrological discontinuities. The high degree of persistence in community structure is discussed.

INTRODUCTION

The Baltic sea is one of the largest brackish water areas in the world, with a simple benthic ecosystem (Elmgren 1978). Duplications of Petersens classical community analysis (weight dominance) gave only two benthic communities in the Hanö Bight (viz. the Macoma balthica and Macoma calcarea communities) (Zenkewitch 1963). Lukšenas (1969) distinguished eight biocoenoses of bottom invertebrates in the southern Baltic based on subjective evaluation of abundance values. Later studies have demonstrated changes in the faunal composition of the Bornholm Basin due to frequent stagnation and oxygen depletion as well as salinity increase (Leppäkoski 1975, Andersin & al. 1978).

The community concept in marine biology has been discussed and questioned for various reasons (see e.g. Stephensen 1973 and Gray 1974). Mills (1969) proposed a pragmatic definition of the word community - 'a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups' - which has been widely accepted (e.g. Field 1971; Boesch 1973; Gray 1974; Elmgren 1978). In his paper Mills used the term association as a synonym of community.

Several quantitative and qualitative studies of macrobenthos have been performed in the southern Baltic and many have also touched the Hanö Bight (Thulin 1922; Demel & Mulicki 1954; Forsman 1956; Tulkki 1965; Leppäkoski 1969, 71, 75). Only Demel & Mulicki used their station values to calculate abundance and biomass values for the whole area.

This study aims at an objective community analysis based on numerical classification, and identifying the environmental factors controlling the distributional pattern of macro-zoobenthos.

For future monitoring programmes the results could be useful, as allocation of sampling stations can be made within different faunal assemblages.

STUDY AREA

The area studied was the Hanö Bight (5100 km^2), southern Baltic (Fig. 1). The area is sloping towards south-east where the Bornholm basin begins. The archipelago in the northern part was excluded, and the vessel used restricted sampling to water deeper than 5 m.

In summer a thermocline is usually formed at 15-25 m. The surface water has a salinity between 7 and 8 o/oo in the whole area. The water mass is, however, stratified with a primary halocline at 50 m and a secondary halocline, the depth of which is fluctuating depending on the stagnation conditions (Fonselius 1967). In August 1975 the secondary halocline was found at c. 70 m. The salinity of the two layers below the primary halocline in 1975 (Persson unpublished) was 8.5 - 12.0 o/oo and 12.5 - 18.0 o/oo, respectively. The stagnations cause lack of oxygen and sometimes formation of hydrogen sulfide. This may affect the fauna deeper than 60 m. (Tulkki 1965; Leppäkoski 1969, 1971).

The bottom substrates in the Bight can be divided into four main types: (1) Coarse sand, mostly with pebbles, dominating in the western part down to 40 m, (Mdø) = -0.12 phi units, (2) Medium and fine sand in the near-shore area and at scattered stations down to 40 m, Mdø = 2.42, (3) Very fine sand, found between 40 and 60 m, Mdø = 3.33 and (4) Silt and clay (mud), at depths > 60 m, Mdø = 6.75.

The ignition loss (550° C, 2 hours) was much lower in types 1 and 2, $\bar{I}$ = 0.8 (n = 17) and 1.0 % (n = 10), than in type 3, $\bar{I}$ = 2.7 % (n = 11) and this in turn was significantly lower than in type 4, $\bar{I}$ = 12.2 % (n = 6). At four of the six stations between 67 and 80 m the sediment had an odour of H_2S in August 1975.

MATERIAL AND METHODS

The study area was divided in five depth strata, 5-19, 20-39 m etc. The number of randomized stations in each stratum decreased with depth in accordance with the lesser variability of the

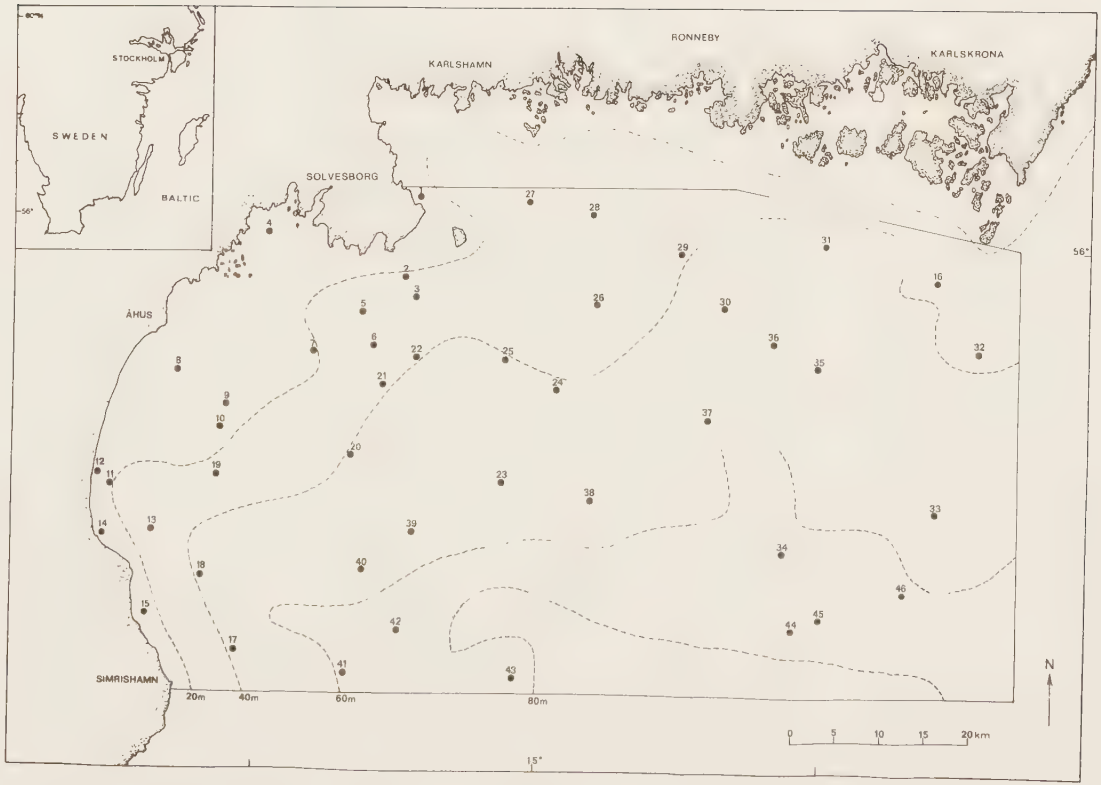

Fig. 1. Area studied with isolines of depth and stations sampled.

bottom substrates found in earlier studies (Persson unpubl.). Three samples per station were taken with a 0.1 m^2 Smith-McIntyre grab, but at bottoms with pebbles the grab sometimes failed and at two stations (3 and 9) no samples were obtained. In all 123 sample units were taken from 44 stations.

The samples were sieved through a 1 mm mesh sieve, and the sieve residues were preserved in 4 % buffered formaldehyde. The animals were identified to species or in some cases to higher taxa (Nematoda, Nemertini, and Oligochaeta).

The individuals from each species and sample were weighed separately after blotting for c. 1 min. on a filter paper. The molluscs were weighed with their shells after opening to remove water in the mantle cavity. The biomass of the polychaeta Pygospio elegans was estimated by using a standard value of 1 mg/ind (Muus 1967).

The area of different depth intervals was calculated by drawing isolines of depth from a marine chart and weighing the different areas.

A numerical classification method was used to group stations and species. Similarity was calculated by Czekanowskis (1913) coefficient, both with presence-absence of species as a basis, and with dominance as a basis.

$$C = \frac{2w}{a + b} \times 100$$

where a is the number of species in the first sample, b is the number of species in the second sample, and w the number of species common to both samples. For dominance the index is equal to the sum of the lowest dominance values for common species. Indices were calculated both with stations as individuals (normal analyses) and with species as individuals (inverse analyses) (Stephenson 1973). The values were then sorted with the group-average method (Mountford 1962) and presented in affinity dendrograms.

Diversity was calculated by means of two indices, namely: the Shannon-Wiener index (Shannon & Weaver 1963)

$$H' = - \sum_{i=1}^{s} p_i \log_2 p_i$$

and the evenness index (Pielou 1966)

$$E = \frac{H'}{\ln s}$$

s = the number of species in the sample.

Subsamples of the sediment for analyses of particle size distribution was determined by dry sieving and the mean particle size was expressed in phi units. Ignition loss was determined after two hours burning in 550° C.

RESULTS

NUMBER OF SPECIES, ABUNDANCE AND BIOMASS

In all 25 species and four groups were found (Table 1). The highest number of species, 21, was found in shallow water (5-19 m). The depth intervals between 20 and 59 m had about the same number of species (13 - 15), while the two intervals between 60 and 80 m only gave 8 species each. At two stations (67 and 80 m) no living macrofauna was found, probably due to low oxygen values.

The highest abundance values were found between 20 and 29 m, ($\bar{X}$ = 2090 ind./m^2), and within the 5-19 m interval ($\bar{X}$ = 1933 ind./m^2). The abundance decreased with depth below 30 m, and between 60 and 80 m mean values of only 75 ind./m^2 were found (Table 1).

The dominating species was Mytilus edulis, which accounted for 25 % of total abundance. Other dominant taxa were Pygospio elegans, Pontoporeia affinis, Macoma balthica, and Oligochaeta. The widest distribution was shown by Diastylis rathkei and Macoma balthica, which were found at 37 and 36 stations respectively. Other species with wide distribution were Harmothoe sarsi, Halicryptus spinulosus, and Mytilus edulis which all were found at 30 stations or more (Table 1).

The highest mean biomass value, 132.04 g/m^2, was found between 20 and 29 m. It was almost twice as high as the second mean value found between 30 and 39 m (Fig. 2).

Mollusca was the dominating group with especially high biomass values (10 - 254 g/m^2) between 20 and 39 m, and amounted to 92 % of total biomass. Crustacea had its highest values (0.3 - 12.0 g/m^2) between 40 and 59 m, while Polychaeta showed high values (0.5 - 6.5 g/m^2) in shallow water.

Table 1. Mean values of abundance (S.E.) of species in different strata in the Hanö Bight 1975, with dominance (D) and frequency (F).

Species / depth, m	5 - 19	20 - 29	30 - 39	40 - 49	50 - 59	60 - 69	70 - 79	D %	F[44]
NEMATODA									
Nematoda spp.			0.3±0.3		0.3±0.3			0.01	2
NEMERTINI									
Nemertini spp.	16.1±5.7	2.6±2.6	0.3±0.3	2.2±1.5	5.3±2.2	8.3±8.3	0.8±0.8	0.42	15
PRIAPULIDA									
Priapulus caudatus Lamarck					0.7±0.7		1.7±1.0	0.02	3
Halicryptus spinulosus Siebold	1.7±0.9	11.9±4.8	34.0±7.6	18.4±4.7	34.0±7.6			1.56	31
Varia Σ	17.8	14.5	34.6	20.6	40.3	8.3	2.5	2.01	
ANNELIDA									
Harmothoe sarsi (Malmgren)	16.5±6.0	29.0±15.6	18.2±6.4	15.4±4.0	15.8±3.7		0.8±0.8	1.39	32
Nereis diversicolor O.F.Müller	178.6±54.5	0.7±0.7						2.94	8
Scoloplos armiger (O.F.Müller)					70.0±42.4	21.5±21.5	36.3±36.3	1.10	6
Pygospio elegans Claparède	604.7±164.7	318.1±142.8	138.6±51.8	44.0±22.1	0.6±0.6			16.83	27
Aricidea suecica Eliason						14.9±14.9		0.06	1
Paraonis gracilis Tauber					2.0±2.0		6.6±5.8	0.06	3
Terebellides stroemi M.Sars		6.0±6.0	64.4±25.4	52.4±18.5	25.1±22.7	1.7±1.7	0.8±0.8	2.61	19
Oligochaeta spp.	596.5±257.9	146.5±95.2	89.8±28.4	4.4±2.3		0.8±0.8		13.17	26
Annelida Σ	1396.3	500.3	311.0	116.2	113.5	38.9	44.5	38.16	
CRUSTACEA									
Diastylis rathkei Kröyer	75.1±26.0	267.3±52.1	131.7±33.1	34.5±8.8	30.4±6.2	9.9±9.9		7.64	37
Seduria entomon L.	1.3±1.3	4.6±2.5	6.9±2.2	5.5±1.7	4.0±1.7			0.35	22
Idothea baltica (Pallas)	0.4±0.4							0.00	1
Iaera albifrons coll. Leach	4.6±2.5	3.3±2.1	2.3±1.6					0.15	7
Gammarus salinus Spooner	24.4±13.4	18.5±7.1	2.3±1.3	0.7±0.7				0.64	14
Calliopius rathkei (Zaddach)	0.8±0.8							0.01	1
Bathyporeia pilosa Lindström	139.4±112.1	8.6±8.6						2.37	5
Corophium volutator (Pallas)	1.3±1.3							0.02	1
Pontoporeia affinis Lindström	2.5±2.1	56.1±48.8	132.7±50.5	389.0±245.4	5.3±4.5			10.59	24
Pontoporeia femorata Kröyer			3.0±2.0	93.5±51.8	153.8±40.8	1.7±1.7		3.38	14
Crangon crangon L.	0.4±0.4							0.00	1
Crustacea Σ	250.2	358.4	278.9	523.2	193.5	11.6		25.15	
MOLLUSCA									
Hydrobia spp.	24.4±15.0							0.40	5
Mytilus edulis L.	132.8±77.7	1063.9±670.5	434.6±168.2	245.5±98.4				26.47	30
Cardium glaucum Bruguière	2.6±2.6							0.03	1
Macoma balthica (L.)	106.4±36.1	152.5±47.1	146.5±46.2	57.6±22.4	42.2±7.9	18.2±18.2	6.6±3.6	7.55	36
Astarte borealis (Chemnitz)					2.0±1.3		20.6±7.6	0.19	5
Mya arenaria L.	2.9±1.9							0.04	1
Mollusca Σ	269.1	1216.4	581.1	301.3	44.2	18.2	27.2	34.68	
Σ/m²	1933.4	2089.6	1205.6	963.1	391.5	77.0	74.2		
Σ species/stratum	21	15	15	13	15	8	8		

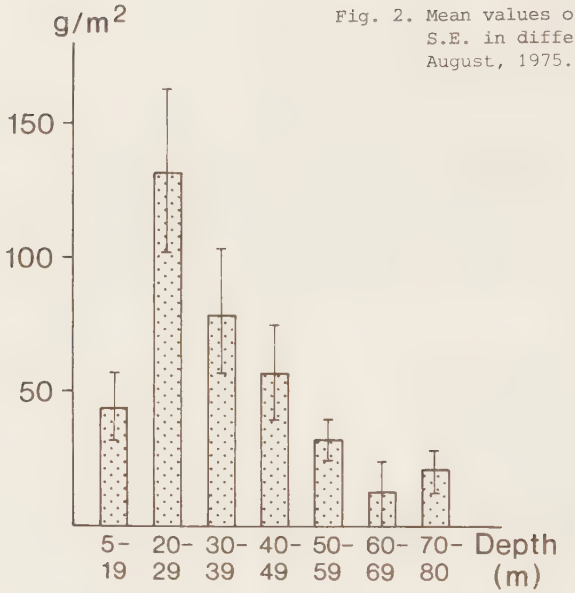

Fig. 2. Mean values of biomass, wet weight, with S.E. in different depth intervals in August, 1975.

The total biomass (standing crop) of macrozoobenthos was calculated to 263 000 tons wet weight. Half of this was found between 5 and 35 m depth (Table 2). This part of the study area made only 30 % of the total area.

COMMUNITY ANALYSES

Classifications based on presence-absence data gave higher similarity levels both for normal and inverse analyses than dominance data (Figs 3-6). In order to get ecologically meaningful groups different similarity levels had to be used in differentiating associations, 70 % for presence-absence and 45 % for dominance. It was then possible to delimit six main associations with the first method and seven with the second. Because of too low similarity values there were seven ungrouped stations in the first case but only two in the second. The distribution of associations showed that in most cases the groups represented distinct areas (Fig. 7 A-B).

Table 2. Standing crop, formalin wet weight, (±S.E.), 10^3kg, of macrobenthos in different depth strata, in the Hanö Bight 1975.

Species / depth, m	5 - 19	20 - 29	30 - 39	40 - 49	50 - 59	60 - 69	70 - 79	Σ
NEMATODA								
Nematoda spp.			0.4±0.4		1.6±1.6			2.0
NEMERTINI								
Nemertini spp.	35.3±13.9	7.3±7.3	2.0±2.0	64.4±43.6	104.0±59.7	64.4±64.4	26.7±26.7	304.1
PRIAPULIDA								
P. caudatus					44.6±44.6		194.4±141.6	239.0
H. spinulosus	25.7±17.2	107.3±26.1	414.2±144.2	230.3±73.9	1489.0±430.0	57.8±57.8		2324.3
Varia Σ	61.0	114.6	416.6	294.7	1639.2	122.2	221.1	2869.4
ANNELIDA								
H. sarsi	96.4±31.7	135.6±79.9	94.7±32.3	332.0±99.7	137.6±40.6		2.3±2.3	798.6
N. diversicolor	1288.3±353.4	2.0±2.0						1290.3
S. armiger					691.7±402.3	91.1±91.1	173.9±173.9	956.7
P. elegans	362.0±118.1	205.3±96.7	90.8±48.5	37.6±21.8	0.7±0.7			696.4
A. suecica						19.8±19.8		19.8
P. gracilis					3.1±3.1		7.9±6.9	11.0
T. stroemi		17.2±17.2	255.8±125.4	482.1±306.9	269.0±239.3	26.1±26.1	2.3±2.3	1052.5
Oligochaeta spp.	312.5±142.9	101.6±64.7	52.8±15.2	4.0±2.0				470.9
Annelida Σ	2059.2	461.7	494.1	855.7	1102.1	137.0	186.4	5296.2
CRUSTACEA								
D. rathkei	275.9±104.3	889.4±215.8	423.7±100.3	252.1±69.0	217.8±53.8	89.8±89.8		2148.7
S. entomon	37.3±37.3	124.4±66.0	402.6±248.5	1247.7±589.4	4505.5±2015.0			6317.5
I. baltica	0.7±0.7							0.7
I. albifrons	1.3±1.3	2.0±1.7	2.6±2.0					5.9
G. salinus	118.1±94.1	79.9±43.2	6.6±4.6	11.4±11.4				216.0
C. rathkei	0.7±0.7							0.7
B. pilosa	141.6±104.3	8.9±8.9						150.5
C. volutator	2.0±2.0							2.0
P. affinis	5.9±5.9	94.7±79.9	262.0±72.6	1479.4±778.5	36.0±27.7			1878.0
P. femorata			6.6±4.3	536.3±282.8	1215.1±398.0	11.6±11.6		1769.6
C. crangon	0.7±0.7							0.7
Crustacea Σ	731.7	1199.3	1104.1	3526.9	5974.4	101.4		12499.3
MOLLUSCA								
Hydrobia spp.	78.9±50.2							78.9
M. edulis	10307.9±8090.0	47554.3±24734.2	18348.3±5877.6	45449.6±18746.3				121660.1
C. glaucum	1488.0±1488.0							1488.0
M. balthica	11449.4±3170.6	28930.1±9359.5	26461.7±8705.7	8231.9±5538.4	22527.5±7390.7	7464.9±7464.9	10.6±6.2	105076.1
A. borealis					2134.8±1936.8		11845.0±4803.2	13979.8
M. arenaria	533.3±357.4							533.3
Mollusca Σ	23857.5	76484.4	44810.0	53681.5	24662.3	7464.9	11855.6	242816.2
Σ	26562.9	78260.0	46824.8	58358.8	33378.0	7825.5	12263.1	263472.1

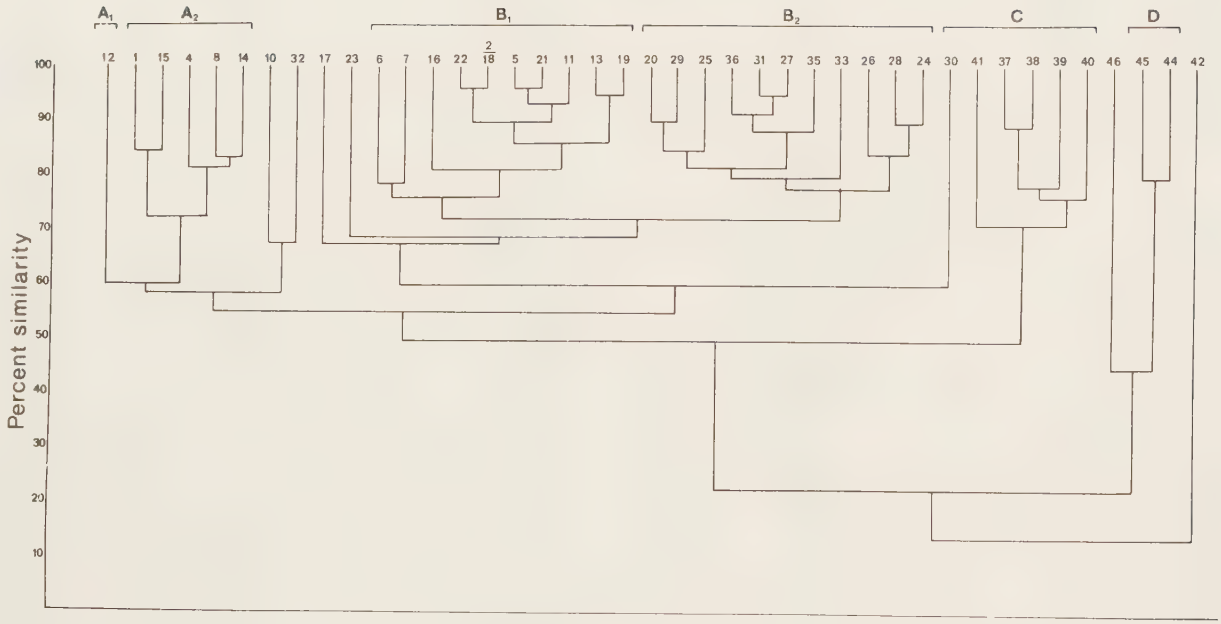

Fig. 3. Dendrogram based on presence-absence data with six associations marked, normal analysis.

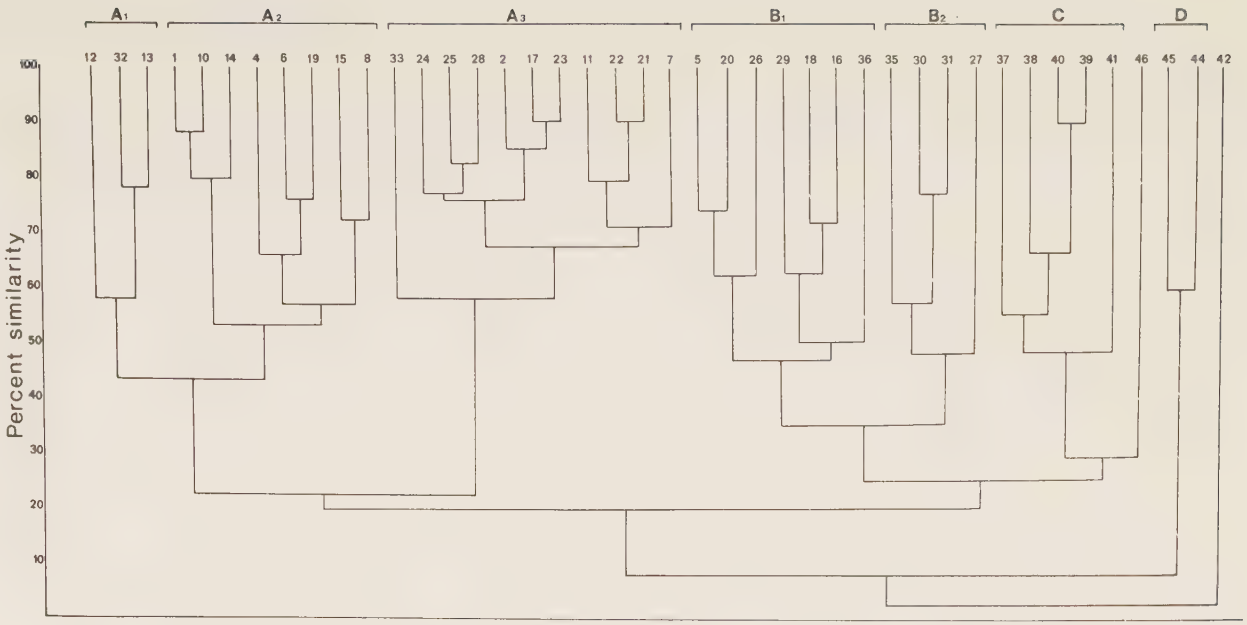

Fig. 4. Dendrogram based on dominance data with seven associations marked, normal analysis.

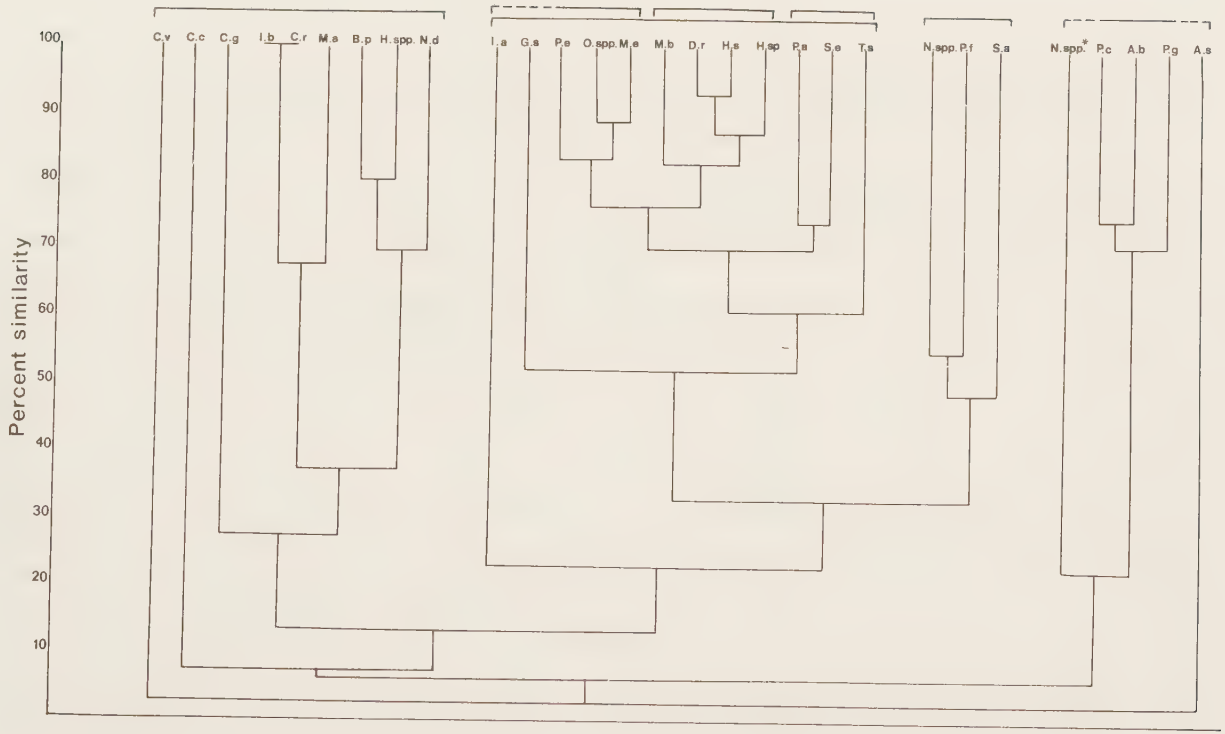

Fig. 5. Dendrogram based on presence-absence data with species groups marked, inverse analysis.
* denotes Nematods spp. See Table 1 for complete scientific names.

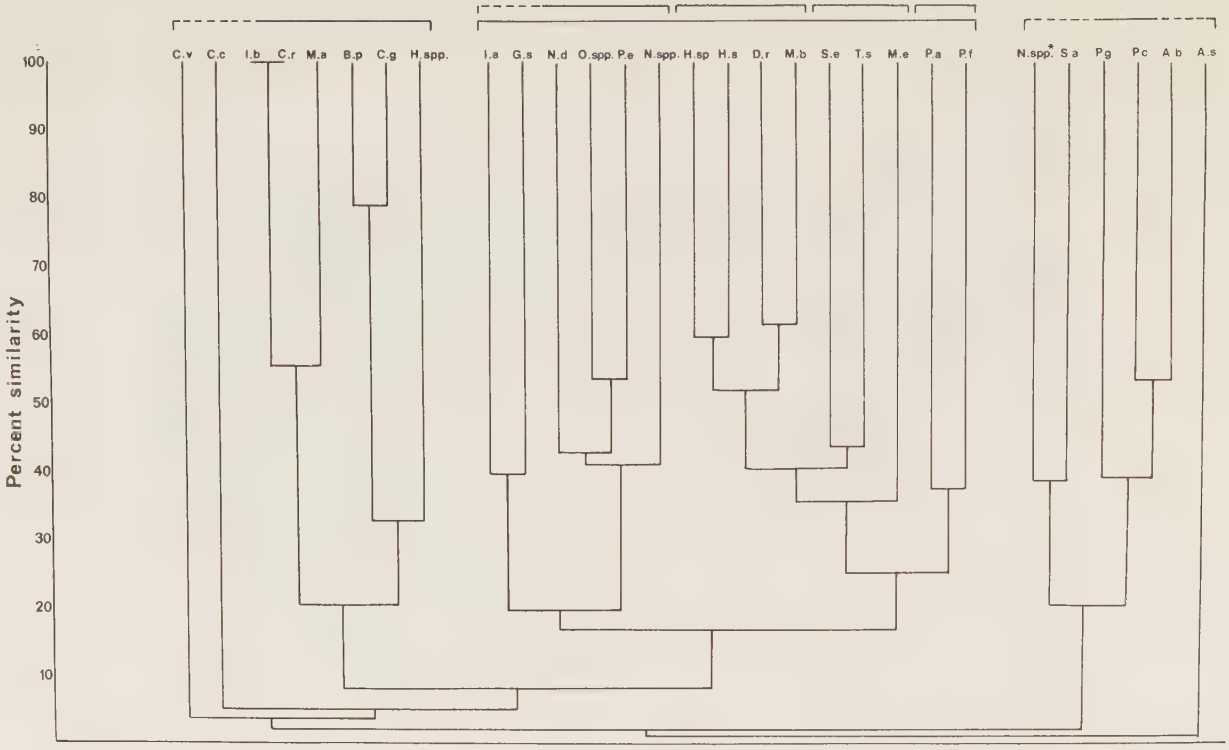

Fig. 6. Dendogram based on dominance data with species group marked, inverse analysis. * denotes Nematoda spp.

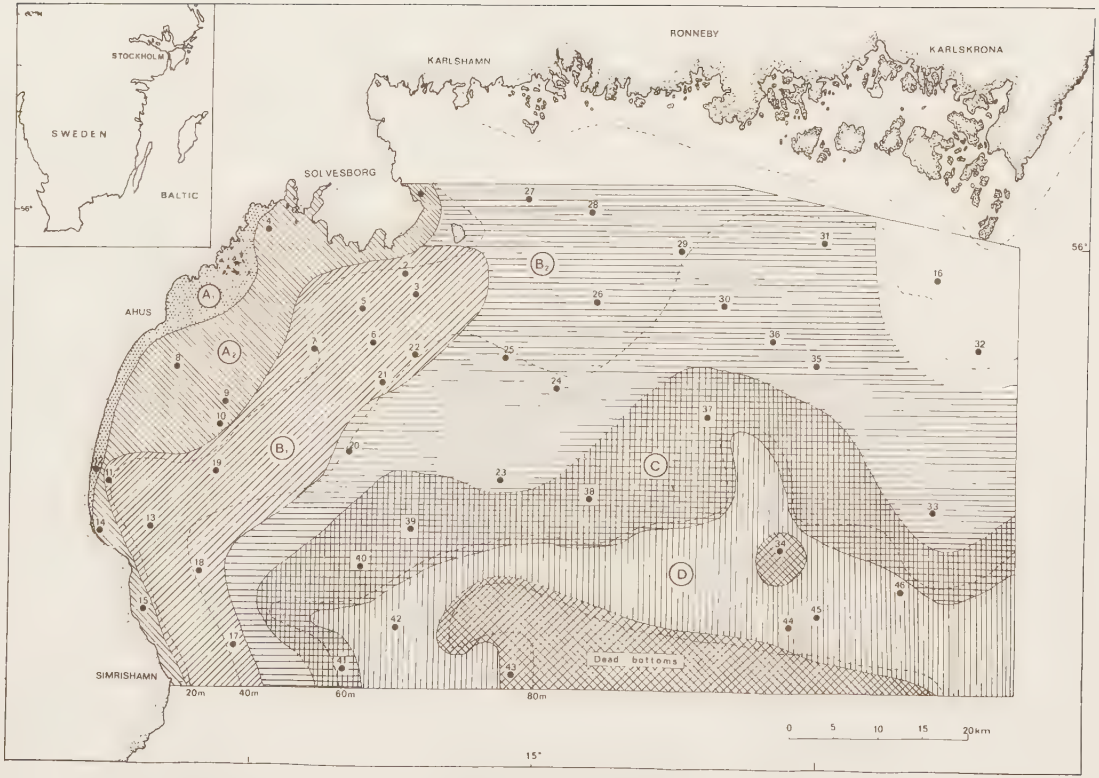

Fig. 7A. Areal distribution of associations in 1975, presence-absence. In areas with low number of stations data from other studies (Persson unpubl.) have been used to delimit the associations.

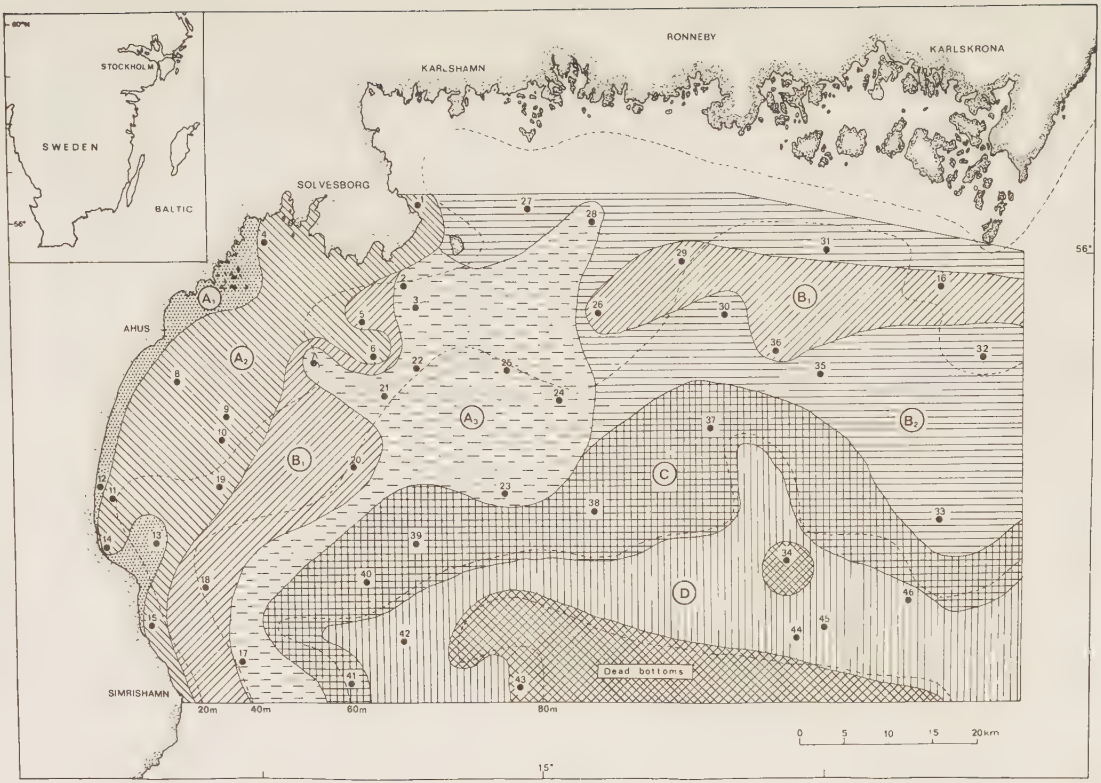

Fig. 7B. Areal distribution of associations in 1975, dominance method. In areas with low number of stations data from other studies (Persson unpubl.) have been used to delimit the associations.

Association A_1 was in both cases dominated by the species Pygospio elegans, Bathyporeia pilosa and Macoma balthica (Table 3), and had a rather low number of species. The mean biomass was about 64 g/m^2. The substrate was fine sand, or fine sand upon coarse sand.

The A_2 associations became also similar with both methods except that the number of stations was five with presence-absence classification and eight with dominance classification. It was a shallow water association with mean depths of 14 and 17 m, and characterized by Oligochaeta spp., P. elegans, and Nereis diversicolor. It was the richest association both in terms of species and specimens but had rather low biomass values, 35 and 54 g/m^2, respectively. The substrate was coarse sand, mostly with pebbles, and the ignition loss was the lowest of all associations, 0.8 and 0.7 %, respectively.

Mytilus edulis and Diastylis rathkei were dominants in associations B_1, presence-absence, and A_3, dominance, which were presented by eleven stations both. The areal distribution of the associations was, however, somewhat different as only five of these stations were common to both associations. The biomass was the highest of all site-groups with mean values of 113 and 106 g/m^2, respectively. The diversity and evenness values were especially low in the dominance classification as the dominance of M. edulis was most expressed there (Table 4). The substrate was less homogeneous, as both fine and coarse sand was found.

Presence-absence classification gave an association of eleven stations (B_2) with a mean depth of 41.5 m and with Pontoporeia affinis as dominant species and M. edulis and Terebellides stroemi as subdominants. The substrate varied between fine and coarse sand. Both diversity and evenness indices were the highest obtained at this classification. On the basis of dominance data the corresponding association became divided in two parts (B_1 and B_2), with mean depths of 36.5 and 45 m. The finest substrate and the highest ignition loss (2.3 %) were found in B_2. The first association was dominated by P. affinis, M. balthica, and D. rathkei, while in the latter P. affinis and Pontoporeia femorata had a very clear dominance.

The two deepest associations were identical with both methods. The first contained P. femorata and Scoloplos armiger as dominants, while the second was characterized by Astarte borealis and S. armiger. The abundance was much lower than in the other site-groups whereas the difference in biomass was less evident.

Table 3. Abundance (A) and frequency (F %) of species in associations derived from presence-absence and dominance data.

P-A ← → D

Association	A_2		B_1		B_2		C		D		A_1		A_2		A_3		B_1		B_2		C		D	
Species	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F	A/m^2	F
Nematoda spp.			-	3			1	7							-	4					1	7		
Nemertini spp.	26	69	1	10	2	19	9	47	1	11			242	60	2	18	-	5			9	47	1	11
P.caudatus							1	7	2	22											1	7	2	22
H.spinulosus	1	15	24	77	28	77	33	87			1	11	4	35	23	65	35	86	18	75	33	87		
H.sarsi	21	85	25	70	19	61	13	54	1	11	1	11	16	70	26	83	15	53	24	83	13	54	1	11
N.diversicolor	238	100	-	3							81	44	149	70										
S.armiger							78	80	48	33											78	80	48	33
P.elegans	673	100	200	80	47	45	1	7			934	100	492	100	81	50	80	86	11	33	1	7		
A.suecica							6	7													6	7		
P.gracilis							2	13	9	33											2	13	9	33
T.stroemi			19	38	94	80	2	13	1	11					45	65	64	62	73	66	2	13	1	11
Oligochaeta spp.	933	92	109	77	41	50					38	56	678	95	32	61	80	72						
D.rathkei	97	92	206	100	62	90	31	74			130	89	91	90	150	94	109	100	15	75	31	74		
S.entomon	2	8	6	38	6	35	2	27			2	11	2	15	5	32	8	43	8	33	2	27		
I.baltica	1	8											-	5										
I.albifrons	6	23	3	22									4	25	3	25	1	5						
G.salinus	15	54	21	51							2	11	13	55	17	32	2	14						
C.rathkei	1	8											1	5										
B.pilosa	40	54	4	10							306	33	25	35			6	14						
C.volutator	2	8											1	5										
P.affinis	4	15	123	61	320	83	1	7			34	33	3	10	72	65	198	96	714	91	1	7		
P.femorata					80	48	129	87							3	11	1	14	239	100	129	87		
C.crangon	1	8											-	5										
Hydrobia spp.	30	46									15	33	19	35										
M.edulis	82	77	707	86	272	64					12	67	144	75	1051	100	21	67	15	17				
C.glaucum											6	22												
M.baltica	121	100	143	100	83	67	43	87	10	24	228	100	116	100	34	58	190	86	33	75	43	87	10	24
A.borealis							2	13	24	56											2	13	24	56
M.arenaria	3	33									3	22	2	15										
A/m^2	2297		1591		1054		354		96		1791		2002		1594		810		1150		354		96	
Spec./ass.	20		16		12		16		8		15		20		15		15		10		16		8	

Table 4. Number of stations in the associations, mean depth, bottom type and community characteristics.

A. Presence-absence classification

Assoc.	N	d	Md Ø	I	S	Ab.	B	H´	E
A_1	1	8.0	2.98	1.9	9	2950	64.7	1.27	0.58
A_2	5	13.6	-0.39	0.8	20	2297	34.7	1.68	0.56
B_1	11	28.5	0.71	0.8	16	1591	112.9	1.77	0.64
B_2	11	41.4	2.30	1.7	12	1054	52.8	1.96	0.79
C	5	56.2	3.15	3.1	16	354	32.0	1.86	0.67
D	2	70.5	6.90	13.6	8	96	28.1	1.37	0.66

B. Dominance classification

Assoc.	N	d	Md Ø	I	S	Ab.	B	H´	E
A_1	3	21.7	1.67	0.9	15	1791	63.6	1.51	0.56
A_2	8	16.9	-0.36	0.7	20	2002	53.5	1.88	0.63
A_3	11	34.3	0.71	1.1	15	1544	105.7	1.29	0.48
B_1	7	36.4	2.23	1.2	15	810	72.1	2.03	0.75
B_2	4	44.8	3.69	2.3	10	1150	16.9	1.24	0.54
C	5	56.2	3.15	3.1	16	354	32.0	1.86	0.67
D	2	70.5	6.90	13.6	8	96	28.1	1.37	0.66

N = number of stations, d = mean depth, Md Ø = medium particle size in phi units, I = ignition loss in per cent of sediment dry weight, S = number of species, Ab. = mean abundance per m^2, B = mean biomass in g wet weight, H´= Shannon-Wiener diversity index, E = evenness.

The inverse classification gave a rough division in three groups, where the largest could be divided in three subgroups. The first group was represented by shallow water species with Bathyporeia pilosa and Hydrobia spp. as most abundant species. With presence-absence data also N. diversicolor belonged to this group.

The second group had a core of the four widely distributed species, viz. M. balthica, Harmothoe sarsi, D. rathkei, and Halicryptus spinulosus. Then there was one group of species with their main distribution in shallow water and occurring down to

40-50 m, with P. elegans, Oligochaeta spp., M. edulis, Iaera albifrons, coll. and Gammarus salinus. The third sub-group comprised species with a main distribution around 40 m with e.g. P. affinis, Saduria entomon, T. stroemi, and P. femorata.

The third group was made up by deep-water species with Astarte borealis and Scoloplos armiger as dominants.

DISCUSSION

The 46 sampling stations in the Hanö Bight did not yield a complete list of species and full details of their distribution. In a monitoring study in 1970-72 (Persson 1976a) comprising 1600 samples from 26 stations between 7 and 75 m depth, 34 species and 8 unidentified taxa were found. But as the species found in the present study made almost 98 % of the dominance of macrobenthos found in the previous investigation, it may be appropriate to discuss species distribution and community structure on the basis of the material.

Some authors have noticed that the number of species, their abundance and biomass are generally increasing with decreasing depth in the Baltic. Berg (1973) found that the number of species decreased from 1 m depth and the abundance from 3 m and downwards. Ankar & Elmgren (1976) found the richest fauna measured by these criteria in the 5-10 m interval. In my investigation the number of species was highest in shallow water (5-19 m), whereas the highest abundance and biomass were found somewhat deeper (20-29 m). Further down the conditions agree with previous studies. The explanation might be that this part of the Hanö Bight has an open and exposed coast with a substrate of fine sand to depths of about 17 m (Persson 1976b), while coarse sand with pebbles are found between 20 and 40 m. These bottoms give a high abundance of Mytilus edulis which influences the biomass values. Outside the Baltic Dörjes (1976) found a species maximum at 40-50 m depth and an abundance maximum at 14-18 m depth in the Helgoland Bight. He correlated this distribution with exposition.

The biomass values agree with other studies in the region. Demel & Mulicki (1954) reported somewhat higher mean values in shallow areas depending on some stations with high dominance of Mytilus edulis. They also had a high biomass in deep water, as Macoma calcarea was still present, and Scoloplos armiger was very abundant due to the favourable oxygen conditions.

In 1967, during Polish IBP investigations in the southern Baltic, seven stations were sampled in the Hanö Bight (Zmudzinski 1969) and gave biomass values below 100 g/m^2 in depths between 20 and 70 m.

One reason for denying the existence of associations in marine biology has been the argument that environmental factors determining species distribution are gradually changing and thereby give populations grading into each other without discrete borders. In the Baltic Sea some hydrographical discontinuities exist, viz. the summer thermocline and the primary and secondary halocline. Elmgren (1978) divided the distribution of macrozoobenthos in three zones depending on the oxygen content in the water. The importance of the halocline as a structuring agent of the marine ecosystem on the Swedish west coast has been shown by Rosenberg & Möller (1979).

Invasion of marine and limnic species into the Baltic is regulated primarily of the extent of euryhalinity (Segerstråle 1957), but due to different zoogeographical origin of the species temperature is equally important in regulating species distribution within the Baltic (Fig. 8). This is probably not due to lethal effect of high or low temperatures, but to its influence on fecundity and reproductive rates (Kinne 1970).

The concepts of global and neighbourhood stability are furthermore of importance in the continua-community controversy. Global stability means that the community returns to the same equilibrium point after perturbations, whereas with neighbourhood stability there exist multiple stable points which are unpredictable and stable only in a small scale (Sutherland 1974; Gray 1977).

The idea of neighbourhood stability implies that biological interactions are most important for structuring communities. In this context the Macoma-Pontoporeia theory (Segerstråle 1962, 1973) has been put forward as an example of a dynamic balance of two dominating species due to interference competition (Gray 1977). However, this relationship has never been properly tested, see e.g. Ankar (1977), Segerstråle (1978).

In the Hanö Bight two species have been found to oscillate in numbers in the 1970s, viz. Cardium glaucum and Diastylis rathkei (Persson 1976b, 1981a). These variations did not show any correlation with population changes of other species. In D. rathkei the abundance in summer was found to correlate with temperature the winter before. Lawton & Strong (1981) have stressed the im-

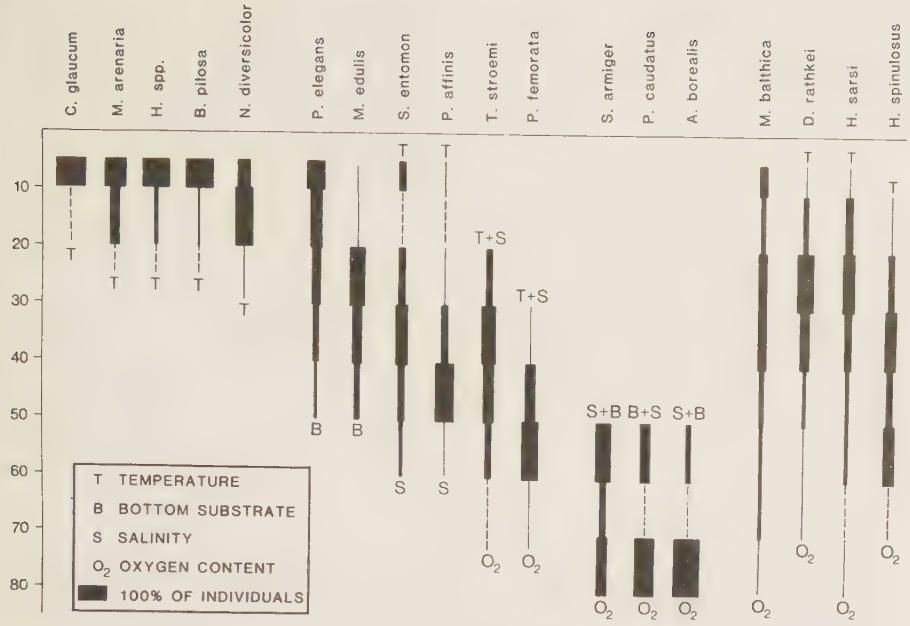

Fig. 8. Depth distribution of important species in the Hanö Bight, with main limiting abiotic factors. ---- individuals found in other studies (Persson unpubl.).

portance of autecological responses of species as an organizing force in communities. As the changes in populations sizes mentioned above were found to be comparable for large areas the results are consistent with the theory of global stability.

In the Baltic highly significant increase in macrofaunal biomass has taken place since the 1920s above the halocline. The possible reasons for this have been discussed by Cederwall & Elmgren (1980) and Persson (1981b). In this context it is important that, in spite of the large biomass change the structure of the community is unaltered, i.e. the same species are found in about the same proportions (Cederwall & Elmgren 1980). Having shown areal and temporal stability in the structure of macrozoobenthos, I propose global stability to be a realistic model for associations above the halocline in the Baltic.

The changed community below the halocline (Leppäkoski 1975) still remains due to the frequent stagnations with oxygen depletion, which does not allow the Macoma calcarea association to reinvade.

In the early 1970s it was assumed that the organisms in the Baltic were exposed to stress due to the low salinity, and as the community also had a low number of species it should be unstable and more vulnerable to additional stress factors, e.g. pollution, than communities in more marine environments. The susceptibility of the Baltic was questioned by Rosenberg (1976) and Järnelöv & Rosenberg (1976), who drew parallels with estuarine ecosystems and emphasized that species already under stress resist additional disturbances better. The Baltic is not, by definition, an estuarine ecosystem and the species are not normally living under stress as they are well adapted to the environment.

The reason for the stability of Baltic softbottom community structure may be the low number of species and the relatively high degree of eurytopy of these species. Eurytopic species are widely distributed and, therefore, achieve high degree of long-term temporal stability in population size (Jackson 1974). Furthermore, the low number of species implies that the number of ecologically related species is very low compared to more marine areas (Dahl 1973). The Pontoporeia-species pair was found to have their maximum abundance in different depth zones (Fig. 8). Ankar (1977) furthermore showed a vertical zonation in the sediment for the two species.

The low number of ecologically related species indicates that interspecific competition is low. With low degree of specialization the niches are overlapping and a reduction in number of one species is not necessarily compensated by an increase of another species but of several species, which makes it difficult to detect. The data presented suggest that clusters of species and sites exist in the Hanö Bight. This structure is, however, most probably not a function of biological interactions among coexisting species but a common response to environmental conditions. The clustering should thus be due to the environmental discontinuities prevailing in the area. It has often been found that distinct discontinuities exist in offshore areas whereas the fauna in inshore areas change gradually (Lie 1978). Kiørboe (1979), however, showed that the distribution pattern of the species changed throughout the year and found distinct communities in Holbæk Fjord only in March.

Regarding the zone between different hydrographical regimes as a discrete limit, its importance is a matter of scale. It might, however, be useful to determine borders between different asso-

ciations to form a basis for future monitoring studies. If these associations are stable in time under natural environmental conditions, it would be more useful to study changes in distribution of the associations than changes in separate stations as a response to anthropogenic changes in the Baltic environment.

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WERE MACROBENTHIC CHANGES INDUCED BY THINNING OUT OF FLATFISH STOCKS IN THE BALTIC PROPER?

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ABSTRACT

Possible causes of longterm increase in macrobenthic biomass in the Baltic proper are discussed.

Eutrophication by means of nutrient enrichment is shown to be a process of the last three decades. It is assumed that primary production has doubled during this time. Macrobenthic data from the southern Baltic indicate highly increased biomass values above the halocline between the 1920s and 1950s. During the last three decades no biomass increase was found. Because of these facts, eutrophication is rejected as a major cause of increased macrobenthic biomass.

Flatfish populations in the southern Baltic were very dense before the 1920s. This resulted in stunted growth due to strong competition for food. After heavy exploitation in the 1920s and the early 1930s, these stocks were thinned out and showed significantly higher growth rates due to the reduced competition. In the late 1930s the catches of cod increased markedly.

Based on evidence from studies of predator-prey relationships it is proposed that the increased macrobenthic biomass values are due to the decreased grazing pressure following the exploitation of the flatfishes. Furthermore, it is assumed that the increase of the stock of cod in the 1930s was due to reduced food competition between young cod and flatfishes, especially the dab.

INTRODUCTION

Man's longterm impact on the terrestrial environment is evident. In aquatic ecosystems this influence is of a more recent origin, and the marine environment was long thought to be almost unaffected. Increasing pollution, however, has been shown locally to change the biota and at the same time over-exploitation of fish stocks led to changes in fish communities. These effects of human activities are mostly regarded as deleterious to the environment.

The fear of irreversible changes in the Baltic because of eutrophication and more recently the spread of toxic substances has led to increased sewage treatment in the surrounding countries. The concern about eutrophication was induced by the increasing frequency of stagnant anoxic bottom water in the Baltic basins which started in the 1950s (Fonselius 1977). The development of anoxic bottom water was thought to be due to increased sedimentation of organic

oxygen-consuming matter or/and changed hydrographical conditions. The problem has not been settled yet, but according to Rydberg (1979) the reason is probably increased oxygen consumption in the bottom water. As nutrients are released from the sediments in anoxic water, thereby increasing the primary production when recycled, the process may be selfregenerating to some extent.

The effects of excessive input of organic matter and nutrients in Baltic coastal waters have been shown by many authors, e.g. Leppäkoski (1975a), Zmudzinski (1976), Landner *et al.* (1977), Varmo & Skog (1980). Up to a certain level macrobenthic standing crop and production are favoured by organic material. Cederwall & Elmgren (1980) have shown that macrobenthic biomass in the central Baltic has been more than fourfolded since the early 1920s. They hypothesized a connection between the biomass increase and the eutrophication. Increased primary production was thought to have increased sedimentation of organic material and thereby increased the food supply for the benthic fauna.

The purpose of this paper is to expand on the theory presented by Cederwall & Elmgren (op. cit.), and to evaluate in more detail the possible effects of major changes in demersal fish populations. I shall try to analyze the time factor in the eutrophication process by presenting some data on the growing nutrient enrichment.

I am grateful to Prof. Per Brinck for critically reading the manuscript. I thank Dr Ragnar Elmgren for giving useful comments as a non-anonymous reviewer. Laborator Gunnar Otterlind and Dr's Rutger Rosenberg and Bo W. Svensson read earlier versions and gave helpful comments. I also thank Mrs Steffi Douwes for drawing the figures and Mrs Ylva Zachrison for typing. Own results presented were obtained in studies financed by the National Swedish Environment Protection Board.

BACKGROUND DATA

Pollution and primary production

Nutrients and organic material are added to the Baltic system mainly through rivers, sewage plants and industrial outlets. Most of the nutrients are coming through rivers and sewage plants, whereas complex organic matter is coming from the pulp and paper industry.

Thorell (1977) calculated the amount of phosphorus and BOD (Bio-chemical oxygen demand) discharged from Swedish urban areas (Fig. 1). There has been a tremendous increase in both parameters up to the late 1960s, when a decline started because of improved sewage treatment. The rate of BOD from industries shows a similar development with the highest values during the 1960s (Hartwig 1977).

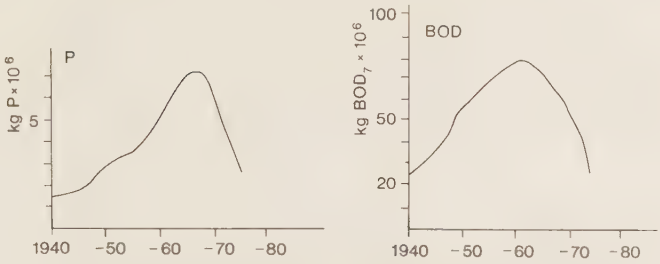

FIG. 1. Amount of phosphorous and biochemical oxygen demand (BOD_7) discharged to the Baltic from urban areas in Sweden, 1940-1975. From Thorell (1977).

Nehring (1979) and Fonselius (1980) summarized data on phosphorous in Baltic surface water during the period 1958-1980, and in an earlier paper Fonselius (1970) presented a few data for 1938-1955. According to these data the phosphate level remained unchanged up to the late 1950s. In the last fifteen years, however, we have had a threefold increase (Fig. 2).

Zmudzinski (1976) supposed that pollution had increased during the last 20 years in the Baltic. This suggestion was based on Polish measurements of nutrients in surface water. According to him this pollution had caused increased primary production in the last ten years.

Data on primary production are scarce until the 1960s. In the Sound there seems to have been a level primary production between the 1930s and 1950s

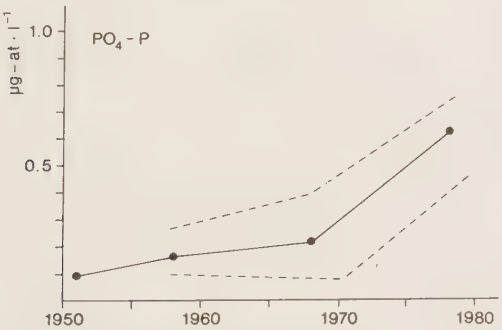

FIG. 2. Mean phosphate contents in the mixed winter surface layer of the eastern Gotland Basin, 1951-1978. Dotted lines show range of values.

(Steemann Nielsen 1937, Steemann Nielsen & Hansen 1961). For the next decade Edler (1977) recorded a 100 % increase, which was suggested to be caused by increasing pollution of the Sound.

Both with respect to discharge data and primary production it thus seems that eutrophication has been most pronounced in the last two decades.

Changes in macrobenthic communities

The sampling area used by various workers are shown in Fig. 3.

The halocline divides the macrobenthic fauna in the Baltic in two different communities. Their longterm development has been quite different. Leppäkoski (1975b) showed that below the halocline in the Bornholm basin (>70 m) a totally different community had developed due to the increasing frequency of stagnating anoxic conditions since the 1950s (see also Tulkki 1965, Leppäkoski 1971, and Andersin *et al.* 1978). Table 1 shows that macrobenthic biomass decreased very much below 90 m depth in this area. The zone between 70-80 m had a very high biomass in the late 1920s, whereas the values from the early 1920s and those of the 1950s and 1970s are much lower.

FIG. 3. Map of the southern Baltic showing investigated areas. 1 = Swedish coast, 2 = Arkona basin, 3 = Bornholm basin, 4 = Oder- and Rönnebank, 5 = Southern midbank, 6 = Hoburg bank and Gotland coast.

TABLE 1. Temporal and spatial variations of macrobenthic biomass, $g \cdot m^{-2}$, from the Baltic proper. Areas listed are deliminated in Fig. 3.

Reference	Swedish coast	Arkona basin	Bornholm basin		Oder- and Rönnebank	Southern midbank	Gotland coast
Thulin (1922)	3.8 (4) 30-40 m	11.6 (7) 40-47 m	14.3 (2) 69-73 m				
Hessle (1924)							6.3 (4) 20-25 m
Hagmeier (1930)		11.2 (4) 40-47 m	193.4 (2) 69-79 m	78.6 (2) 94-96 m	24 + 3.2 (9) 7-30 m	18.5 (3) 22-35 m	
Demel & Mulicki (1954)	27 + 379 (5) 18-36 m	55.9 (6) 40-47 m	21.5 (5) 72-79 m	7.3 (4) 90-94 m	34 + 41 (7) 6-37 m	53 + 419 (5) 15-38 m	18 + 31 (2) 20-25 m
Löwe (1963)	41-42 (8) 23-38 m	34.3 (38) 40-48 m			41-118 (41) 8-30 m		
Leppäkoski (1969)				0.6 (1) 92 m			
Sasdy (1978)	30 + 4.0 (8) 20-30 m						
Persson (1977, *unpubl.)	37 + 42 (18) 8-30 m	55.6 (5)* 46-47 m	16.1 (5) 70-80 m				
Cederwall & Elmgren (1980)							50.4 (4) 20-25 m

When two values are given for biomass the second represents the biomass of *Mytilus edulis*.
Figures in brackets indicate number of stations.

In the Arkona basin an increase of the biomass has been registered since the 1920s. The increase occurred before the 1950s (Table 1). This is due to an increase of some species, especially species of *Astarte*, and colonization of *Arctica islandica*. According to Hagmeier (1930) the distribution limit for the last mentioned species was, in the late 1920s, the Mecklenburg bay, western Baltic.

Above the halocline, three quantitative investigations exist from the 1920s, which can be compared with data from the last three decades (Table 1). The values of Thulin (1922) and Hessle (1924) from the early 1920s are very low; the mean biomass values are below 10 $g \cdot m^{-2}$. Hagmeier (1930) reported increased values in the late 1920s. He found 27.2 and 18.5 $g \cdot m^{-2}$, respectively, from the Oder-Rönnebank and the southern Midbank. In the early 1950s, Demel & Mulicki (1954) recorded considerably increased biomass values for the various subareas, ranging from 49.0 to 495.0 $g \cdot m^{-2}$. The increase was mainly due to *Mytilus edulis*, but it is evident also when this species is disregarded.

The studies from the 1970s are less extensive than those in the 1950s, but a comparison is possible and makes it very clear that no biomass changes were recorded. Mean biomass values (without *Mytilus*) in subarea 1 were 27.0 and 41.0 $g \cdot m^{-2}$ in the 1950s (Demel & Mulicki 1954, Löwe 1963), which are very close to those found in the 1970s, viz. 29.9 and 36.8 $g \cdot m^{-2}$, respectively (Sasdy 1978, Persson 1977). The values reported by Cederwall & Elmgren (1980) from the central Baltic are also within the range of those from the southern Baltic. When extrapolating the mean dominance of *Mytilus edulis* at all their stations above the halocline to be valid for those in the compared depth interval a biomass of 24.8 $g \cdot m^{-2}$ (without *Mytilus*) can be calculated.

The data indicate that there was an increase of the biomass of benthic macrofauna above the halocline in the Baltic between the 1920s and 1950s.

Changes in the exploitation of demersal fish populations

In the Baltic, five commercially important species of demersal fish are found, viz. plaice (*Pleuronectes platessa*), flounder (*Platichtys flesus*), dab (*Limanda limanda*), turbot (*Psetta maxima*) and cod (*Gadus morrhua*). With the exception of the turbot, the exploitation of the stocks have shown large fluctuations during the 20th century.

Swedish investigations in 1913-1921 showed that the southern Baltic had very large populations of flounder, plaice and dab, whereas the cod population was rather small (Ekman 1916, Molander 1925). Therefore, an important fishery for flatfish started in 1922 (Molander 1926).

In the beginning, only the plaice was exploited. The total yield of plaice in the southern Baltic in the years 1918-1920 amounted to 243 metric tonnes per year, and increased to 4500 metric tonnes per year in 1924-26 (Johansen 1928). This high yield of plaice was followed by a decrease around 1930. Since then

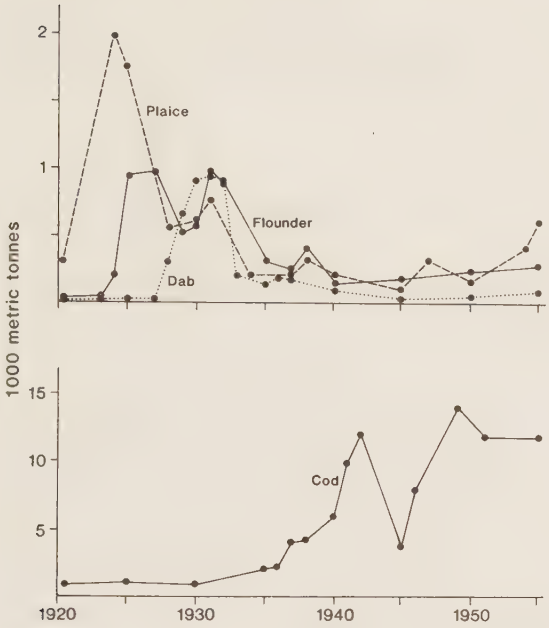

FIG 4. Danish catches of plaice, flounder, dab and cod in the Baltic proper. Redrawn after Jensen (1959).

only some years have given high yields due to strong year classes (cf. Fig. 4). Trends in catches from other countries have been the same, except that German catches of cod were high during the early 1940s.

Around 1925 an intense fishery for flounder commenced in the southern Baltic, mainly carried out by Danish and Swedish fishermen. High yields were obtained for about ten years until a decrease took place.

The dab was heavily exploited for a rather short period in the late 1920s and early 1930s. During these years 800 tonnes were caught per year, to be compared with about 50 tonnes per year before. According to Ekman (1916) the dab was the dominating flatfish in the southern Baltic, and rather big populations were found around Gotland by Hessle (1923). Today the stock is very thin, even in the southern Baltic (Arntz 1971, Otterlind, pers. comm.).

The yield of cod was low in the southern Baltic until the middle of the 1930s, when it began to increase rapidly. The catch increased until the 1950s (Jensen 1959). During the last two decades only minor fluctuations have occurred, probably due to changes in the fishing effort (Otterlind 1980).

Changes in growth and age of demersal fishes

The rich populations of flatfish found in the southern Baltic in the 1910s consisted mainly of old individuals with stunted growth (Ekman 1916, Molander 1925). Similar conditions prevailed in 1906 according to Strodtmann (1926).

Marked changes in growth rate were found already in the middle of the 1920s (Hertling 1928). This trend then continued to the late 1930s. Fig. 5 shows how the length of a four-year old individual increased with about 75 % during that period.

Data on growth rate of cod are rare and marked changes were not found. However, some data exist which indicate a somewhat better growth of young cod of today compared to those of the 1930s (Kändler 1944, Tiews 1974). Older fish, however, have had a slightly reduced growth rate in later years.

The age composition of the flatfish populations changes simultaneously with the thinning-out of the stocks, as is shown for plaice and flounder in Fig. 6. In 1922, over 90 % of the catch of the plaice consisted of individuals of five years or older, whereas in 1930 > 90 % of the catch were younger than five years.

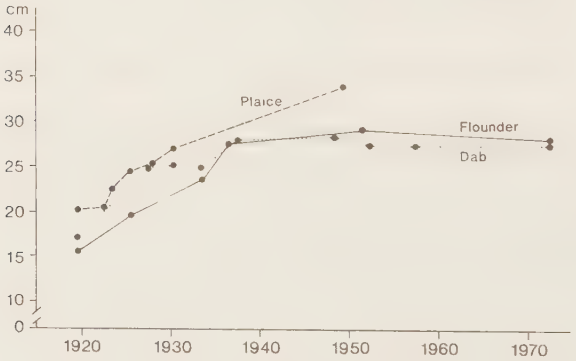

FIG. 5. Changes in mean length of 4-year old specimens of plaice, flounder and dab in 1919-1973 in the southern Baltic.

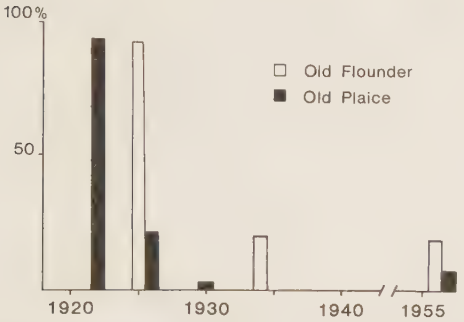

FIG. 6. Age composition of plaice and flounder in commercial catches in the Bornholm area. Old >4 years.

The same trend was found in the flounder catches between 1925 and 1935. Altnöder (1939) reported that in 1921, 47% of a plaice catch from the Arkona basin were eight years or older, compared to only a few per cent in the 1930s.

Demersal fish and food composition

The above-mentioned three species of flatfish are specialized for feeding on macrobenthic food items, mainly crustaceans and molluscs. The percentage composition varies somewhat in different areas due to the available prey (Table 2). Flounder and dab both prefer crustaceans, with *Bathyporeia pilosa* and *Gammarus* spp. being most important for the flounder, and *Pontoporeia* spp. for the dab. Fish are unimportant as food, but according to Hessle (1923), the dab often feeds on roe.

According to the data in Table 2 the cod prefers small crustacean species. However, other non-quantitative studies stress the importance of *Mesidotea entomon* and fish in the south and central Baltic (Hertling 1928, Hessle 1923).

DISCUSSION

Thanks to the pioneering work of the Danish biologist, C.G.J. Petersen, quantitative data on benthic standing crop exist since the beginning of the present century. Due to the importance of the fishery, much data are also available on fish stocks during the same period.

Two papers on long-term conditions of macrobenthos in Swedish waters were published recently. Rosenberg & Möller (1979), discussing data from the

TABLE 2. The composition of the food of plaice, flounder, dab and cod from the southern Baltic (above the halocline). Percentages of numbers of food items.

	Ref. & Sampling year	Food items				
		Mollusca	Polychaeta	*Mesidotea entomon*	Crustacea	Fish
Plaice	(1) 1925	65.6	6.8	0.1	27.4	0.1
	(1) 1926	66.0	1.6	0.1	22.2	0.01
Flounder	(1) 1925	19.0	6.7	0.1	74.4	–
	(1) 1926	29.5	0.4	0.2	69.7	0.01
	(2) 1971	2.6	14.3	–	82.7	–
	(3) 1976	56.0	5.0	1.0	38.0	–
Dab	(1) 1925	10.0	2.2	0.5	86.2	0.9
	(1) 1926	21.6	3.9	2.7	70.7	0.2
	(4) 1968	16.2	28.6	–	47.2	0.05
Cod	(5) 1968	4.3	9.6	–	85.7	–
	(6) 1968	13.0	21.6	–	60.2	3.9
	(3) 1976	1.0	12.0	4.0	80.0	2.0

(1) Hertling (1928), (2) Arntz (1977a), (3) Olofsson & Hagberg (1977), (4) Arntz (1971), (5) Arntz (1974), (6) Arntz (1977b).

west coast of Sweden, compare the 1920s with 1976, and Cederwall & Elmgren (1980) compare the early 1920s with 1976-77 in the central Baltic. Rosenberg & Möller (l.c.) concluded that differences found in abundance and biomass were artifacts due to the treatment and seasonal and interannual variations in the material. Cederwall & Elmgren (l.c.), however, claimed the changes in biomass to be due to eutrophication resulting from increased primary production. In both cases increase of biomass was reported for the 1970s.

A comparison of macrobenthic data from different periods is difficult for various reasons. Different sampling devices may have been used. Petersen grabs were used in the studies of the 1920s and 1950s, whereas Smith-McIntyre grabs were used in the 1970s, except by Rosenberg & Möller and Cederwall & Elmgren. The latter sampler gives somewhat higher biomass values as it cuts deeper into the bottom (Gallardo 1965). The samples were sometimes taken at different seasons, but this is probably less important in the Baltic, since biomass is dominated by long-living molluscs. Cederwall & Elmgren (1980) were able to compare the same stations, whereas my data from the southern Baltic are representative only for certain areas and depth intervals. Because of the high number of stations investigated in the 1950s (19-49) and the 1970s (8-18) small-scale patchiness may not, however, have influenced the results.

Present data show that a marked increase in macrobenthic biomass has occurred since the early 1920s in the southern Baltic. This agrees with the results presented by Cederwall & Elmgren (1980) from the central Baltic. Furthermore, the data given by Demel & Mulicki (1954) and Löwe (1963) indicate that the increase in the southern Baltic mainly took place before the 1950s.

When discussing the cause of the benthic biomass increase Cederwall & Elmgren (l.c.) stressed that no long-term data on primary production exist. Data on nutrient enrichment are very limited too, but the phosphorous values given by Thorell (1977) indicate a marked increase after the 1940s. The increased phosphorous load in the 1950s and 1960s fits well with the increased phosphorous values of the Baltic surface water given by Nehring (1979) and Fonselius (1980). Phosphorous may not be the limiting factor in the Baltic, but it seems probable that other nutrients present a similar pattern. Furthermore, the primary production data from the Sound (Steemann Nielsen 1937, Steemann Nielsen & Hansen 1961) show that the increased primary production took place during the last two decades. This is also stressed by Zmudzinski (1976) for the southern Baltic.

It has been shown (Mills 1975) that there is no simple first order relation between primary production and production of the benthic community. In a model, Ursin & Andersen (1978) found that a 100 % increase of phophorous in the North Sea within a ten-year period gave a 13 % increase of primary production and a 5 % increase of invertebrate production. Assuming a P/B ratio of 1.0 as a mean for benthic macrofauna in the Baltic this would mean that the fourfold increase found for biomass by Cederwall & Elmgren (1980) should be caused by a 13-fold increase of primary production.

In my opinion the above data do not support the hypothesis that the increased standing crop of macrobenthos in the Baltic has been caused by eutrophication.

Cederwall & Elmgren (1980) assumed that the predation pressure on macrobenthos was lower in the 1920s due to less dense fish stocks. Based on present data I shall try to evaluate possible changes in the stocks feeding on macrobenthos.

Dense, slow-growing populations of flatfishes were common in many areas before rationalized fishing methods were developed (Petersen 1920, 1922). There are no reliable quantitative estimates of the south Baltic flatfish stocks, but for a comparable situation in the Belt Sea Petersen (1922) estimated the stocks to be 100 times larger before the exploitation period. From data presented by Molander (1937) a reduction of stock size with at leat 10 times can be calculated for the flounder at the Swedish south coast.

The extremely slow growth of individuals in the southern Baltic was noticed by e.g. Hessle (1923) who, however, found that flounder in some places at Gotland had a somewhat higher growth rate than in the southern Baltic. Generally, the increased growth rates following the heavy fishing were claimed to be due to reduced competition for food after thinning-out of the stocks (e.g.

Hertling 1928, Molander 1937, 1955, Jensen 1959). There is a great overlap in food choice between the three species of flatfish in the Baltic as a consequence of the low number of food species. All the macrofauna species except big individuals of *Astarte* spp. and *Arctica islandica* are preyed upon by the flatfishes. Recent studies of Arntz (1978, 1980) have shown the strength of this competition. He also demonstrated that strong competition exists between the dab and young cod.

Although the reduced predation pressure was well known, no one seems to have analyzed the impact of this change on the macrobenthos. Already Blegvad (1928) realized that dense stocks of plaice in the outer part of Limfjorden reduced the standing crop of the food animals to a minimum. In cage experiments he found a 60-fold increase in population density of food animals during the summer period when predators were excluded. In long-term studies of macrobenthos in Limfjorden he demonstrated that the amount of first class plaice food was constantly low in that part of the fjord which contained large stocks of plaice (Blegvad 1951), in contrast to other areas. Virnstein (1977) concluded from cage experiments that predation pressure keeps many populations below the level of carrying capacity of the environments.

Large-scale examples of predator-prey relationships affecting the abundance of macrobenthic fauna have been reported from marine (e.g. Boddeke 1978, McIntyre 1978) as well as limnic areas (e.g. Bidgod 1973, Stenson 1979).

The annual exploitation of benthic food resources by demersal fishes in the Kiel area was estimated to amount to 20 % of the annual production (Arntz 1980). He calculated the mean fish density to one fish per 30 m^2. As was mentioned above, the density of the unexploited flatfish populations in the southern Baltic was probably much higher and would have implied a heavy grazing of the macrobenthic fauna.

Based on the above data on changes of the density of fish populations, their growth rate and grazing pressure, I conclude that the increase of macrobenthic standing crop in the southern Baltic above the halocline was a result of the thinning-out of the flatfish populations.

In the central Baltic the density changes of fish stocks seem to have been less evident, but data are scarce. Less dense populations in the 1920s are indicated by the growth data given by Hessle (1923). On the other hand, more recent data show that the growth rate of flounder has increased also in this area (Zemskya 1959). Furthermore, the dab population has almost disappeared from the Baltic proper and macrobenthic grazing decreased below 30 m depth.

Cederwall & Elmgren (1980) demonstrated that the biomass in the Fårösund was as high in the 1920s as in the 1970s. This should be related to the information given by Hessle (1929) that the most intense flounder fishery at Gotland was carried out in the Fårösund. Hessle (l.c.) also noted that the population had higher growth rate than populations outside the sound.

These facts indicate that the increased standing crop of macrobenthos also in the central Baltic may be caused be reduced predation pressure – from flounder and dab – and not by the eutrophication process.

The increased standing crop of macrobenthos found at the Swedish west coast (Rosenberg & Möller 1979) cannot, however, be explained by changes in the flatfish stocks. In this area these stocks were thinned out already in the nineteenth century (Petersen 1893). Besides, these macrobenthos communities are more diverse and contain many species not used as fish food (Blegvad 1925). Rosenberg & Möller (op. cit.) also dismissed eutrophication as a cause of the increase, as neither the number of species nor the community structure and dynamics indicated any pollution effects in the 1970s. Such effects are not indicated in the Baltic offshore stations above the halocline either. McIntyre (1978) reviewed long-term variations in macrobenthos for the North Sea. The changes found could be explained by identifiable events such as storms or severe winters. It was concluded that no eutrophication could be demonstrated for the period 1920-1975.

In this connection it is tempting to speculate about the causes of the sudden increase in the catches of cod in the southern Baltic in the 1930s. Estimates of the stocks are not available, but data given by Ekman (1916) and Strodtman (1926) indicate low densities in the southern Baltic. Some authors (Alander 1949, Dementjeva 1959) assumed immigration of young cod to have taken place in the 1930s, but Thurow (1974) considered the increased catches to be due to increased fishing effort only.

Dementjeva (1959) assumed that the increased density of the cod was due to enhanced reproduction conditions after more frequent inflows of saline water. This may be true when stagnating anoxic conditions exist in the spawning area (the Bornholm basin), but this was very rare until late in the 1940s. The reproductive conditions might in fact have been more favourable before this period. Thurow (1974) summarized data which indicate that growth rate of young cod has increased and growth rate of old cod decreased in recent time compared to the 1930s. According to Arntz (1974) young cod preferably feed on crustacea, whereas older cod rely more on fish. Thus, it seems possible that young cod was suppressed by the dense flatfish populations existing until the early 1930s. This assumption implies that young cod are inferior to old flatfish when competing for food.

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